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THE LIFE HISTORY OF TIMOTHY

By

MORGAN W. EVANS
Associate Agronomist, Office of Forage Crops, Bureau of Plant Industry

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INTRODUCTION

The data on which this bulletin is based have been obtained in a life-history study of timothy (*Phleum pratense* L.), which has been conducted, as time has been available, through a period of 12 years, from 1912 to 1924.[1] The greater part of the work was done at the timothy-breeding field station, which is conducted cooperatively by the United States Department of Agriculture and the Ohio Agricultural Experiment Station. For a few years previous to 1915 this station was located at New London, Ohio. In 1915 it was transferred to its present location at North Ridgeville, Ohio.

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[1] In May, 1920, a thesis by the writer entitled "The Life History of Timothy" was placed on file in the library of George Washington University. This paper represents the original thesis, which has been rewritten and to which considerable new data have been added.

The writer wishes to acknowledge aid that has been received from different sources. References to various publications consulted are presented in the "Literature cited." Helpful criticisms and suggestions have been received from Albert Mann, of the Carnegie Institution of Washington; Mrs. Agnes Chase, Lyman Carrier, G. N. Collins, C. V. Piper, and especially R. A. Oakley, of the United States Department of Agriculture. Without their cooperation and also that of other persons not mentioned in this list this bulletin could not have been completed in its present form.

GEOGRAPHICAL DISTRIBUTION

The genus Phleum includes about 10 species inhabiting the Temperate Zones of both hemispheres (*2*, *p. 102*).[2] Of these species only one, *Phleum alpinum* L., is native of North America (*18*, *p. 140*); it is of little economic importance. *Phleum pratense* L., which is native to Europe and northern Asia, and which now commonly grows wild as well as in cultivated fields throughout the humid parts of the northern United States and southern Canada, was introduced probably from Europe (*29*, *p. 122*).

ECONOMIC IMPORTANCE

Timothy grown alone or in mixture with clover is the most important meadow grass in the northeastern part of the United States. It is also grown extensively in the more humid parts of the Northwest, and to some extent on irrigated land there. According to the Fourteenth Census of the United States, timothy in 1919 was grown alone on 10,941,347 acres, and in mixture with clover it was grown on 19,349,405 additional acres (*34*, *p. 796–797*).

DEFINITIONS

Since some of the terms used in this discussion have been employed elsewhere with different meaning and others are new, it seems desirable to define the exact way in which they are used here.

Seedling.—The young plant which develops directly from the seed. The young plant is regarded as a seedling up to the time when lateral shoots appear, or until internodes of the primary shoot become elongated.

Plant.—Includes all growing shoots which have developed from a single seed or from the detached vegetative part of another plant. In a plant several years old there may be a number of growing shoots, or groups of shoots, connected by the nonliving, more or less disintegrated basal parts of shoots which were growing in preceding years. These separate yet closely associated shoots and groups of shoots, which have had a common origin even though they are not vitally connected, are together regarded as a single plant.

Shoot.—Includes a stem with its attached roots, leaves, buds, and inflorescence.

Each bud is a potential branch or lateral shoot. The term " shoot " may be applied from the time when the bud has expanded and both leaves and roots have developed. Shoots which produce inflorescences are fertile; those which do not produce inflorescences are described as sterile shoots.

Innovation.—The name applied to a young shoot which has developed from a bud up to the time when branches develop on it, or until its upper internodes begin to become elongated.

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[2] Serial numbers (italic) in parentheses refer to " Literature cited," p. 53.

Stem.—The axis of the shoot; it includes the proaxis, haplocorm, culm, and rachis.

Proaxis.—The part of the stem below the first elongated internode, or below the haplocorm.

Haplocorm.—The swollen part near the base of the stem. It is usually composed of one, less frequently two, and rarely three swollen internodes.

Culm.—The part of the stem which is composed of elongated, cylindrical, usually hollow internodes.

Since it is desirable to have specific names for the proaxis and the haplocorm, it seems better to restrict the name "culm" to that part of the stem which is composed of elongated, cylindrical internodes. In the upper part of the culm these internodes are hollow, but near the base they are often nearly or entirely solid.

Head.—The inflorescence, which is a spikelike or contracted panicle.

GROWTH OF THE TIMOTHY PLANT

The seeds of timothy mature in northern Ohio in late July or early August. When timothy grows under natural conditions the seeds fall to the ground, and within a few days or weeks, when conditions become favorable, may germinate. Where timothy grows in uncultivated places, and where climatic conditions are similar to those in northern Ohio, volunteer seedlings are likely to develop during August or early in September.

After the seed has germinated the following growth of the plant depends upon the weather, soil conditions, crowding by other seedlings, etc. If growth is comparatively vigorous a bud in the axil of one of the leaves may develop into a secondary shoot. Sometimes, under favorable conditions, four or five, or even more of these secondary shoots may be formed on a plant during the autumn months.

During the cold weather of winter the plant is more or less dormant. In extremely cold weather the upper or tip portions of the blades may be destroyed to some extent by freezing. On the other hand, it has been observed that during periods of mild weather growth of the timothy plants may be resumed temporarily at any time during the winter. This fact is illustrated by records which were obtained from eight timothy shoots in the winter of 1918–19. During the period from December 20 to January 13 a new leaf formed on one shoot but there was no increase in the number of leaves on the others. From January 13 to February 13 one additional leaf developed on each of seven of the eight timothy shoots which were being observed. Table 1 gives records from the United States Department of Agriculture Weather Bureau station at Cleveland, Ohio, at approximately the same altitude as the timothy-breeding field station and at a distance of 22 miles from it. These records show that the weather during the second period, when the greatest amount of growth occurred, was warmer than during the first of these two periods.

TABLE 1.—*Comparison of temperature, sunshine, and precipitation during stated periods at Cleveland, Ohio*

Items of comparison	Dec. 20, 1918, to Jan. 13, 1919	Jan. 13, to Feb. 13, 1919
Mean maximum temperature .... degrees Fahrenheit..	36.4	39.9
Mean minimum temperature .... do....	24.3	28.5
Mean temperature .... do....	30.3	34.2
Sunshine .... hours..	47.6	150.7
Total precipitation .... inches..	0.92	0.53

As soon as spring weather becomes favorable, continuous growth begins again, and for a time the plant develops in about the same way as in the preceding autumn. After a few weeks, or about May 1 in the latitude of northern Ohio, a decided change occurs. Up to this time the nodes which have formed are close together, the internodes being too short to be readily distinguished; the length of this part of the stem, which has been named the "proaxis," is usually less than half an inch. In late spring, however, the younger internodes above it become elongated to form the haplocorm and culm. The final length of the entire stem with inflorescence may be 4 or 5 feet.

The florets bloom in northern Ohio during late June and early July (*9*, *p. 299–309*). The seeds mature in late July or early August, in a little less than a year after the plant may have begun its growth.

Timothy shoots with elongated stems and with mature heads on which seeds matured have been observed to develop, where soil and climate have been favorable for growth, from seed sown in the spring of the same season. Their behavior resembled that of annual plants. Under natural conditions, however, timothy seeds usually germinate, not in the spring, but in late summer or early fall, and seeds are produced on the plant in the following season. In ordinary agricultural practice timothy is not sown in the spring for the purpose of producing a crop, either of hay or of seed, in the same season.

If the life of a timothy plant were ended when it has produced a crop of seed it would be classed as a winter annual, like winter wheat or rye (*28*, *p. 81*). However, after a timothy plant has matured seed it continues to produce branches vegetatively by means of buds at or near the base of the shoots. It is for this reason that timothy is generally classed as a perennial, but it is not a perennial in the same sense that a tree or shrub is perennial. In the case of a tree, although the small flowering twigs may die back after the fruit has matured, the perennial stem or trunk continues growth year after year. On a timothy plant there is no truly perennial part; new stems, with new roots, develop from buds each season.

There is not much evidence available to indicate how long a timothy plant may continue to grow through the vegetative reproduction of new shoots. Some plants selected at Pullman, Wash., in 1907, which were transferred to New London, Ohio, in 1910, then to North Ridgeville, Ohio, in 1915, are still making a vigorous growth. Plants which lack vigor or which are susceptible to rust are likely to cease growth whenever conditions become unfavorable, but those which make a vigorous, healthy growth may apparently continue to grow, at least under favorable conditions, for an indefinite period.

THE SEEDLING

A timothy seedling as it appears a few days after the seed has germinated is illustrated in Figure 1.

When a timothy seed germinates, first the coleorhiza or root sheath expands. The plumule, inclosed in the coleophyll, next appears (*13, p. 24–25*). Soon afterwards the radicle or primary seminal root (*a* to *e*, fig. 1) breaks through the coleorhiza. Filaments closely resembling root hairs develop on the coleorhiza and also upon the minute epiblast (*25, p. 57–60*). There is usually but one seminal root in timothy, though sometimes a second one develops.

From the nodes at the base of the primary shoot of the plant another set of roots appears (at *b*, fig. 1). These roots, as well as those which grow from the base of other shoots which develop later, are called nodal or adventitious roots.

The organ connecting the seed and the base of the primary shoot is the mesocotyl (*a* to *b*, fig. 1). Roots rarely if ever grow from the mesocotyl of timothy, though short appendages resembling root hairs commonly develop from it.

The leaves of the growing bud of the plumule are inclosed within the sheathlike coleophyll (*b* to *c*, fig. 1).[3] Within a few days after the coleophyll has developed, the tip of the first leaf blade emerges and gradually unfolds (*c* to *d*, fig. 1).

There is considerable difference of opinion among plant morphol-

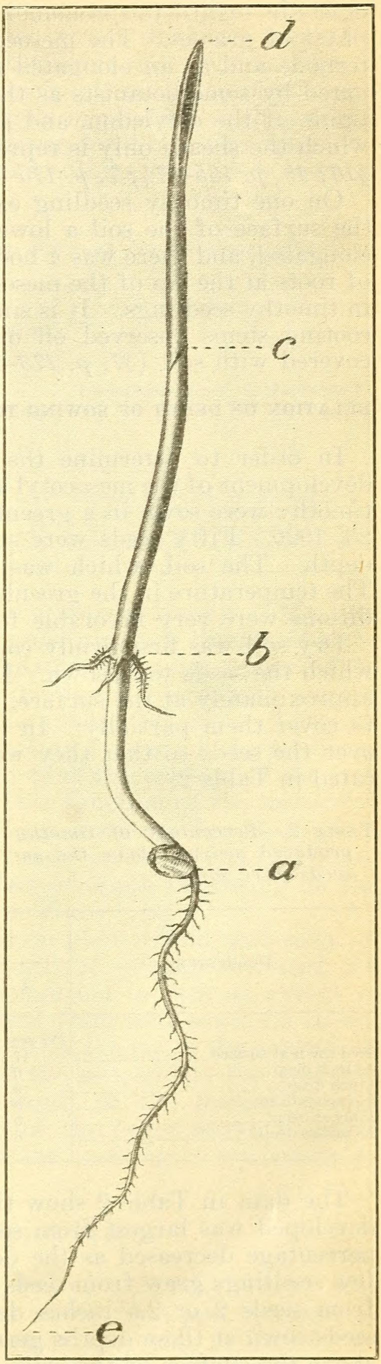

FIG. 1.—A timothy seedling (enlarged): *a* to *e*, Seminal root or radicle; *a* to *b*, mesocotyl; *b* to *c*, coleophyll; *c* to *d*, upper part of first leaf with blade

ogists in regard to the homology of the mesocotyl and of the coleophyll of grasses. The mesocotyl has been regarded both as an internode and as an elongated node. The coleophyll has been designated by some botanists as the cotyledon, by others as the enlarged ligule of the cotyledon, and again by others as an ordinary leaf in which the sheath only is represented (*24*, *p. 7–26; 12*, *vol. 2*, *p. 414–416; 19*, *p. 165–174; 7*, *p. 175–183; 39*, *p. 179–182*).

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[3] Coleoptile has been used more commonly than coleophyll. Both are Greek derivatives. Coleoptile is compounded from the words meaning "sheath" and "feather"; coleophyll from "sheath" and "leaf." Coleophyll is evidently the name which best describes this part of the timothy plant.

On one timothy seedling examined which did not grow through the surface of the soil a lower internode of the shoot was slightly elongated, and there was a nodal root 0.4 of an inch above the whorl of roots at the tip of the mesocotyl. This type of elongation is rare in timothy seedlings. It is similar to the elongation of underground rooting stems observed on older timothy plants which have been covered with soil (*37*, *p. 173–178*).

RELATION OF DEPTH OF SOWING TO GROWTH OF MESOCOTYL AND COLEOPHYLL

In order to determine the effect of depth of sowing upon the development of the mesocotyl and of the coleophyll, seeds of ordinary timothy were sown in a greenhouse at different depths on December 23, 1920. Fifty seeds were sown in each of duplicate pots at each depth. The soil, which was a loam, was kept continually moist. The temperature in the greenhouse ranged from 48° to 60° F. Conditions were very favorable for germination and growth.

Dry soil was first firmly compacted in the pots up to the level at which the seeds were sown. In two of the pots the seeds were sown approximately at the surface, enough soil being scattered over them to cover them partially. In the other pots enough soil was placed over the seeds so that they were at approximately the depths indicated in Table 2.

TABLE 2.—*Percentage of timothy seeds sown at different depths which had produced growth above the surface of the soil on different days after the seeds were sown*

Depth sown	Number of days after sowing							
	8	11	13	15	18	22	29	34
	Per cent	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*
Seed sown at surface	17	41	53	55	57	57	57	57
0.5 inch deep	0	21	43	46	48	48	48	48
1 inch deep	0	3	19	30	34	34	34	34
1.5 inches deep	0	0	0	1	2	4	5	5
2 inches deep	0	0	0	0	0	0	0	0
2.5 inches deep	0	0	0	0	0	0	0	0

The data in Table 2 show that the percentage of seedlings which developed was largest from seeds sown at the surface and that this percentage decreased as the depth of sowing increased. Relatively few seedlings grew from seeds 1.5 inches below the surface and none from seeds 2 or 2.5 inches deep. Although large numbers of the seeds sown at these depths germinated, they did not produce growth above the surface of the soil.

A series of measurements was made of the timothy seedlings referred to in the preceding paragraphs and of some others growing in another series of pots from seed sown at about the same time and at the same depths. The average actual distances measured along the axes of the seedlings from the seeds up to the surface of the soil, the average lengths of the mesocotyls and coleophylls, and the position of the tips of the coleophylls in relation to the surface of the soil are presented in Table 3. Seven seedlings were measured from seeds sown 1.5 inches deep and 10 seedlings from seeds sown at each of the other depths.

TABLE 3.—*Effect of sowing timothy seed at different depths upon growth of seedlings*

Approximate depth of sowing	Average actual distance of seed below surface of soil (inches)	Average length (inches)			Average position of tip of coleophyll
		Mesocotyl	Coleophyll	Total	
At the surface	0.03	0.02	0.21	0.23	0.20 inch above the surface of the soil.
0.5 inch	.52	.46	.24	.70	0.18 inch above the surface of the soil.
1.0 inch	.97	.72	.35	1.07	0.10 inch above the surface of the soil.
1.5 inches	1.50	.91	.53	1.44	0.06 inch below the surface of the soil.

On 6 of the 10 plants from seeds sown approximately at the surface the mesocotyl could not be distinguished, since the nodal roots grew on the axis of each one of these plants at a point very close to the seed. As the depth of sowing increased, the length of the mesocotyl increased to an average maximum of 0.91 inch. Through this organ within certain limits the rooting system of the seedlings of timothy tends to become established near the surface of the soil, irrespective of the depth of sowing. This function of the mesocotyl has also been observed in wheat (*Triticum aestivum* L.; *16, p. 408*), corn (*Zea mays* L.; *6, p. 293–302*), and Sudan grass (*Sorghum sudanense* Piper; *35, p. 8–9*). The effect of depth of sowing on the length of the mesocotyl is illustrated in Plate 1, *A*.

The average length of the coleophyll on plants from seed sown at the surface was 0.21 inch. As the depth of sowing increased the coleophyll also increased in length, though not to such an extent as did the mesocotyl. On the average plant from seed sown 1.5 inches deep the coleophyll was 0.53 inch long. It is the tip of the coleophyll that penetrates through the surface of the soil, unless the seed has been sown so deep that the total length of the mesocotyl and coleophyll is not sufficient for the tip of the latter organ to reach the surface of the soil, in which case the seedling is not likely to grow above it (*8, p. 554*).

VEGETATIVE REPRODUCTION

There is one bud in the axil of each leaf of a timothy shoot. The buds in the axils of the first few leaves which form and the buds at nodes between the elongated internodes of the culm ordinarily do not develop so that they can be detected by the unaided eye, but according to Nishimura their presence can be shown by a microscopic examination of these nodes (*25, p. 61–62*).

Although there may be buds which can be readily observed in the axils of 10 or more leaves at the base of a shoot, seldom if ever does every one of them grow into a lateral shoot. On plants growing under very crowded conditions, or which for other reasons are lacking in vigor, often none of the buds develops into an innovation. On more vigorous plants in timothy meadows a shoot may produce one or two, less frequently more, lateral shoots. Usually these lateral shoots grow from the buds at the one or two nodes immediately below the haplocorm or from the node just above it, rather than from buds at other nodes. When the plant is growing under exceptionally favorable conditions a single shoot may produce from five to seven, or even more, lateral shoots.

Buds may grow into shoots at any time, yet in meadows where there is a dense stand of plants it is not until about midsummer, after the seeds on the fully grown stems approach maturity and the leaves become dry, that the buds at the bases of the stems become more active. As the buds enlarge, the sheaths of the first leaves become elongated and the blades unfold, roots develop, and the branch becomes an independent shoot (*3, p. 20*). A young timothy shoot or innovation which developed from a bud on an older shoot is shown in Plate 2, *B*.

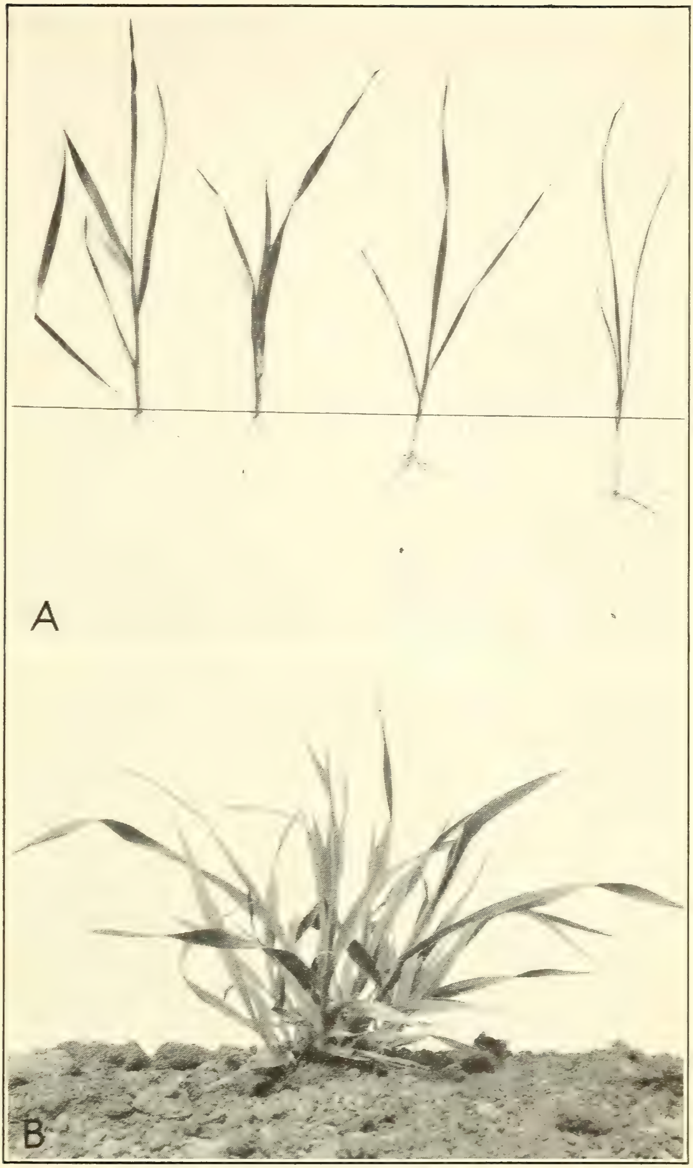
INCREASE IN SIZE OF PLANT

The appearance of typical timothy plants grown from seeds at different stages of development is illustrated in Figure 1 and in Plates 1 and 3.

Grasses are commonly classified in two groups: (1) Turf forming, of which Kentucky blue grass (*Poa pratensis* L.) may be considered a typical example; and (2) bunch forming, of which orchard grass (*Dactylis glomerata* L.) is an example. Although timothy resembles orchard grass more nearly than Kentucky blue grass in its manner of growth, at the same time the plants are generally less compact than in orchard grass.

Although timothy plants growing under normal conditions do not spread by means of rooting stems like the turf-forming grasses, yet the size of the plant does tend to increase somewhat as it becomes older. The proaxes are usually more or less procumbent, growing outward from the center of the plant. As buds in the upper part of the proaxis and also frequently a bud at the node above the haplocorm develop into shoots, the circumference of the plant tends to become greater. In a timothy meadow where the plants were examined October 3, 1914, new shoots were found rooted 1 inch farther from the center of the plant than the older shoots from which they developed, though on most of the plants in this meadow the distance was less than 1 inch.

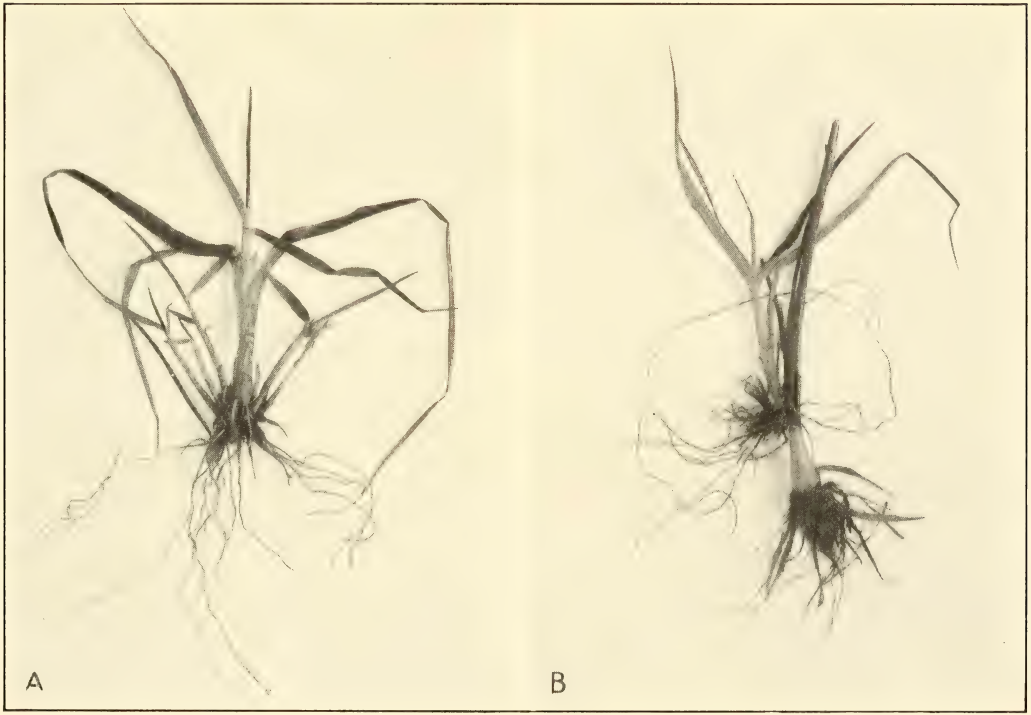
Under unusual conditions underground rooting stems or rhizomes may develop in timothy. When plants are covered with a few inches of soil, there is sometimes an elongation of one or more of the lower internodes which normally would not become elongated. There is thus a rooting stem by means of which the terminal bud of the shoot becomes established near the surface of the soil. The name "topothete" has been suggested for rooting stems of this type in timothy and other grasses (*27, p. 173–178*).



TIMOTHY PLANTS GROWN FROM SEED

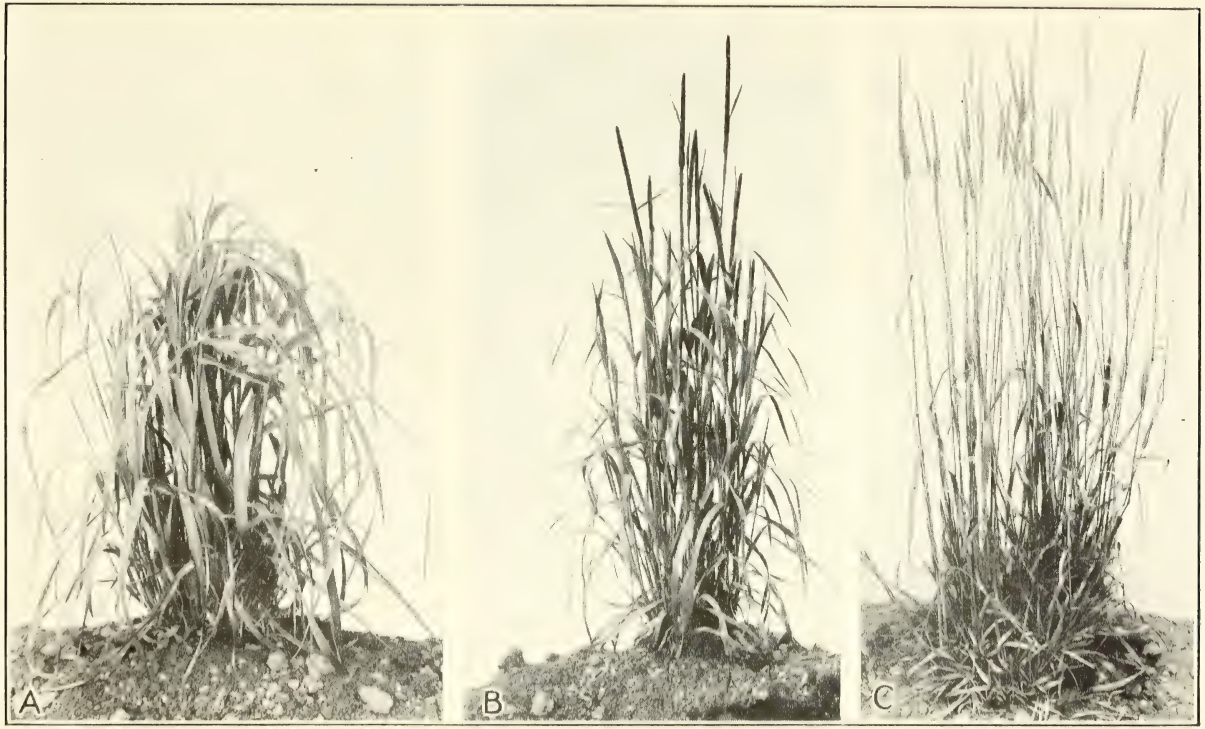
A.—Timothy plants grown from seed sown at varying depths. The surface of the soil is indicated by the straight line. The plant at the left was grown from seed sown at the surface; the second plant at a depth of 0.5 inch; the third, 1 inch; the fourth, 1.5 inches. The length of the mesocotyl increased as the depth of sowing increased. The seed from which each plant grew is attached to it at the base of the mesocotyl, which extends up to the base of the shoot where the nodal roots have developed

B.—A timothy plant grown from seed sown in the autumn of 1922. It was located in an isolated position where it had ample space for growth. This is an illustration of the manner in which a timothy plant increases in size through the development of new shoots in the axils of the leaves at the bases of the older shoots. (Photographed June 1, 1923)



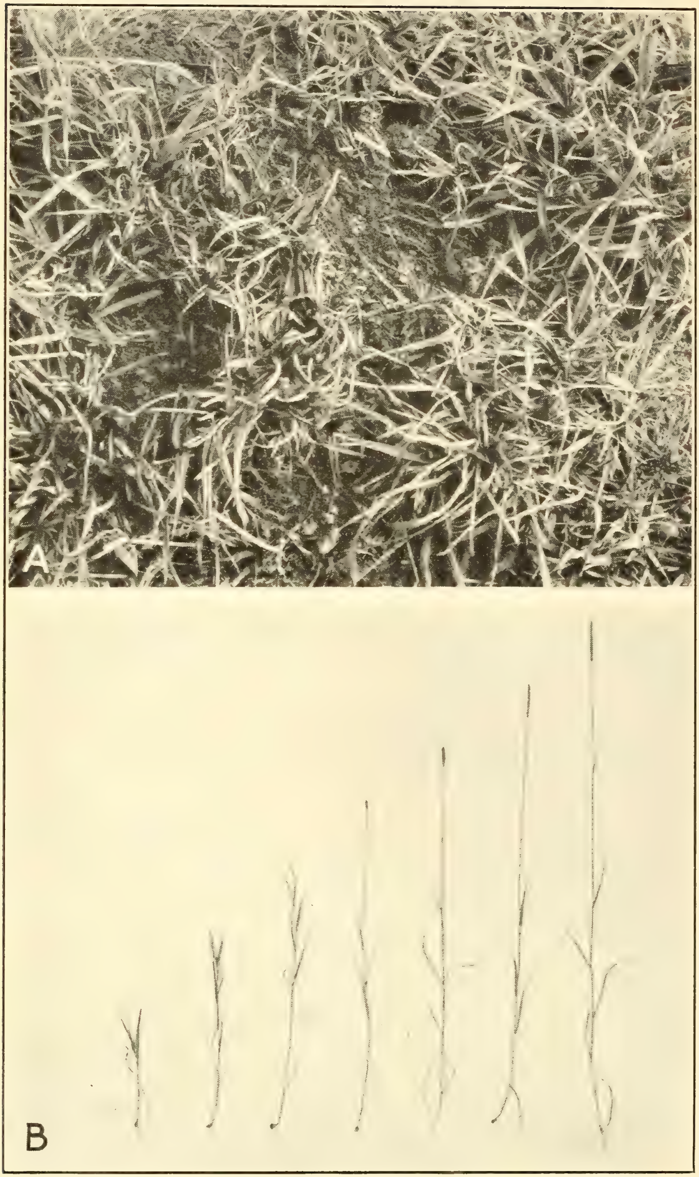
TWO FORMS OF TIMOTHY

A.—Timothy plant with six lateral shoots, three on each side, which have developed in the axils of alternate leaves
B.—A young lateral timothy shoot or innovation with a well-developed root system. It is no longer dependent on the primary shoot, which has ceased growth



TIMOTHY PLANTS AT DIFFERENT STAGES OF GROWTH

A.—A timothy plant, photographed June 11, 1920, after internodes of culms had become partially elongated but before heads had appeared
B.—A timothy plant with heads partially emerged from upper leaf sheaths
C.—A timothy plant grown in a cultivated row plat where conditions were favorable for a large and vigorous growth (photographed July 30, 1923, when growth of stems with heads had been completed and when seed was about to mature).
(A and B are about one-eighth and C about one-twelfth actual size)



A.—A typical area in a timothy meadow in December, 1918, more than three years after it was sown. Between some of the plants there are small areas of bare soil instead of a continuous turf like that which would be produced by Kentucky blue grass and some of the other turf-forming grasses

B.—Timothy shoots of various types. At the right are two typical timothy shoots with heads and at the left three sterile shoots as they appear in midsummer. Between these groups are two shoots having smaller heads and a larger number of leaves than appear on normal shoots with heads; they represent gradations between sterile shoots and typical shoots with heads

The size to which a timothy plant may grow after a few seasons depends very largely upon the space available for its development.

In the fall of 1917 timothy plants, each of which at that time consisted of a few clons from a selected plant, were transplanted 3.3 by 3.3 feet apart in rows where they were afterwards cultivated and hoed each season. On February 28, 1923, these plants were examined. Relatively few of the plants had died; a small proportion of them were about the same size as when transplanted; most of them had become much larger, many of them being from 10 to 15 inches in diameter at the surface of the soil, and some were still larger. In any timothy plant which has been growing in a cultivated row for one or two seasons, usually practically all of the space within its periphery is occupied by a dense growth of living shoots. A conspicuous feature of such plants, which had been growing in cultivated rows through five seasons, was that in a large proportion of them the centers were occupied only by dead roots and stubble, around which the growing shoots were located in formations suggesting "fairy rings." In some of these older plants the growing shoots formed a continuous ring, and in others it was broken at one or more places. In one of the larger plants examined, the largest diameter of which was 18 inches and the smallest 16 inches, there was an area 8 inches in diameter in the middle with only dead shoots, around which the living shoots were growing in a practically unbroken ring.

Where plants are growing in ordinary meadows they do not become as large as in cultivated rows. Sometimes a plant 2 or 3 years old growing in a dense stand may have but a single growing shoot. In the 2-year-old and 3-year-old meadows which were examined October 3, 1914, it was found that where the stand of timothy was not very dense, while the shoots of some of them occupied an area 2 or 3 inches in diameter, most of the plants were smaller.

Although in a meadow timothy plants spread outward to some extent as they become older, yet the areas occupied by adjacent plants ordinarily do not overlap as in fields of some other grasses which form dense turfs. Each plant in a timothy meadow usually remains more or less separated from adjoining plants. This condition is shown in Plate 4, *A*.

ARRANGEMENT OF LEAVES AND SHOOTS

Buds and secondary shoots, like the subtending leaves, are arranged in two ranks, succeeding ones being on alternate sides of the primary shoot. This arrangement is illustrated by the plant shown in Plate 2, *A*.

The leaves on the secondary shoots grow in a plane which is at right angles to that in which the leaves of the primary shoot are growing. This is also shown by the lower leaves with short blades in the shoots at the left side of the central one in Plate 2, *A*.

If the plant is situated where there is ample space for development and if other conditions for growth are favorable, buds in the axils of the leaves of the secondary shoots may also develop into a third set of shoots. The leaves of this third set of shoots are normally in a plane at right angles to the plane in which the leaves of the secondary shoot are growing. Under usual conditions, however, as the shoots and leaves grow and their position becomes determined according to the space for their development, they become so twisted from their normal position that the arrangement as described above may not be easily recognized.

THE SHOOT

It has already been stated that a timothy shoot originates in either one of two ways: (1) Directly through germination and growth from the embryo in the seed; (2) from a bud in the axil of a leaf.

GROWTH IN LENGTH OF STEM

It has been observed in northern Ohio that about the 1st of May (though this date varies somewhat with different seasonal conditions) the upper internodes of the shoots of timothy begin to become elongated. Shoots which have developed from buds late in the preceding summer make nearly all their growth in length during a period of 10 or 11 weeks, after about the 1st of May.

On any timothy shoot which produces an inflorescence each phytomer, or vegetative unit, has been formed relatively early in the spring, before the shoot has made more than slight, if any, appreciable growth in length (*40, p. 44*).

In late spring or early summer in any meadow where there is a dense stand of plants, large numbers of shoots may be found which have ceased growth and become dry. In one meadow where the growth of timothy was comparatively dense, 21 shoots were marked in May, 1916, for observation later in the season. On July 25 it was found that only 13, or 61.9 per cent, of the shoots had continued growth up to that time. In cultivated rows, on the other hand, where each plant has ample space for growth most of the shoots produce culms.

Shoots may become elongated in smaller numbers at any later time during the summer or fall, in the aftermath which grows in meadows after the first crop of hay has been harvested, if soil and weather conditions have been favorable for growth. When culms develop late in the fall, growth is often checked by cold weather before they have attained their full length. It has been found that in northern Ohio these partially elongated culms do not survive the winter. Six slightly elongated culms were observed November 11, 1914, and another group of 13 slightly elongated culms on November 8, 1916. None of them in either group were growing in the following spring.

During the spring of 1916 a series of measurements was made of the stem of one shoot on each of 14 timothy plants. The first measurements were made on May 8, after growth in length had already begun. The average lengths (in inches) of these stems, not including the proaxes on dates when measurements were made, are as follows: May 8, 2.6; May 15, 3.1; May 23, 3.7; June 5, 8.7; June 12, 13.6; June 19, 22.3; June 26, 29.7; July 5, 39.1; July 10, 41.4; July 17, 41.5; July 24, 41.5. The same data are presented in graphic form in Figure 2.

The length of the elongated internodes on the first dates when measurements were made was actually somewhat less than these figures indicate, for the reason that until the tip of the head appeared each stem was measured from its base to the tip of the sheath of the upper unfolded leaf, which at that time extended above the tip of the upper elongated internode. In another series of measurements made on May 8 it was found that the average length of the elongated part of the stem, including the head, of 10 shoots collected from the same meadow, was 0.2 inch. After that date the actual length of the elongated part of the stem gradually approached the figures just presented.

In the early part of May, growth in length of the stems was comparatively slow. Most of the growth in length took place during a period of approximately six weeks, from about May 23 to July 5. Growth continued, though less rapidly, until about July 10.

In the same timothy meadow, the first florets were observed to be in bloom June 24. On June 30 the plants in the meadow were in full bloom and continued so on different days up to July 8. The data obtained in this field show, therefore, that growth of timothy stems is comparatively rapid during the early part of the blooming period and that some growth in length continues up to about the time when the florets are through blooming.

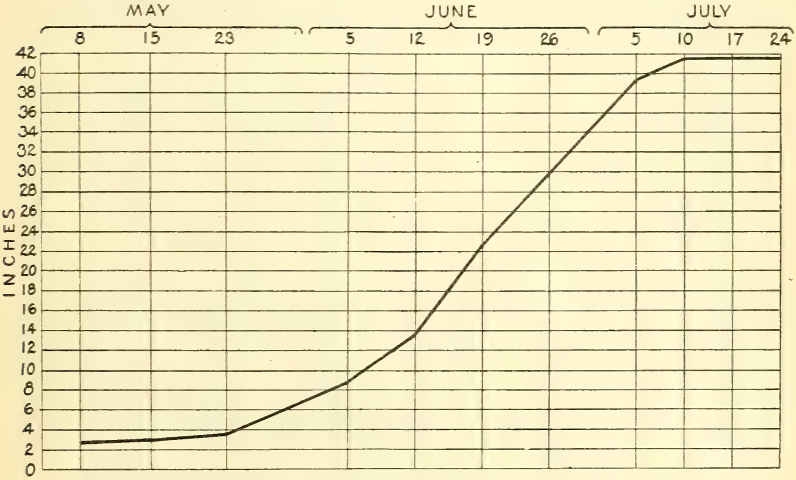


FIG. 2.—Curve showing time and rate of growth of timothy stems

RELATIVE TIME WHEN DIFFERENT INTERNODES BECOME ELONGATED

During the same period in which the data presented in the preceding paragraphs were obtained, another series of measurements was made of the lengths of the different elongated internodes of timothy stems. Ten fertile shoots with heads were examined on each date. Since it was necessary to dissect the shoot in order to obtain an accurate measurement of each internode, a new group had to be used each time. Consequently, the data in Table 4 and the graph in Figure 3 show some slight irregularities in the lengths of the internodes on succeeding dates, which would not have occurred if it had been possible to use the same group of shoots for measurement each time.

TABLE 4.—*Record of average length of the elongated internodes of 33 timothy shoots having six elongated internodes each, collected from an old meadow on eight different dates in 1916*

Date	Number of shoots included in the average	Average length (inches) of internodes					
		No. 1	No. 2	No. 3	No. 4	No. 5	No. 6
May 29	1	0.20	1.50	2.10	0.30	0.10	0.06
June 5	3	.80	2.76	3.20	.90	.16	.26
June 12	7	.56	1.26	3.37	3.92	1.90	2.69
June 19	6	.49	1.91	3.52	6.41	5.91	7.10
June 26	6	.68	2.85	4.63	6.46	8.16	10.25
July 3	4	.55	1.70	3.37	5.65	9.77	15.20
July 10	3	.82	2.70	4.82	7.32	11.22	17.42
July 18	3	.63	1.86	4.86	6.00	9.70	19.33

The lowest elongated internode has been numbered 1, and those above it follow in numerical order. The length of the upper one was measured from the node at its base up to the base of the head.

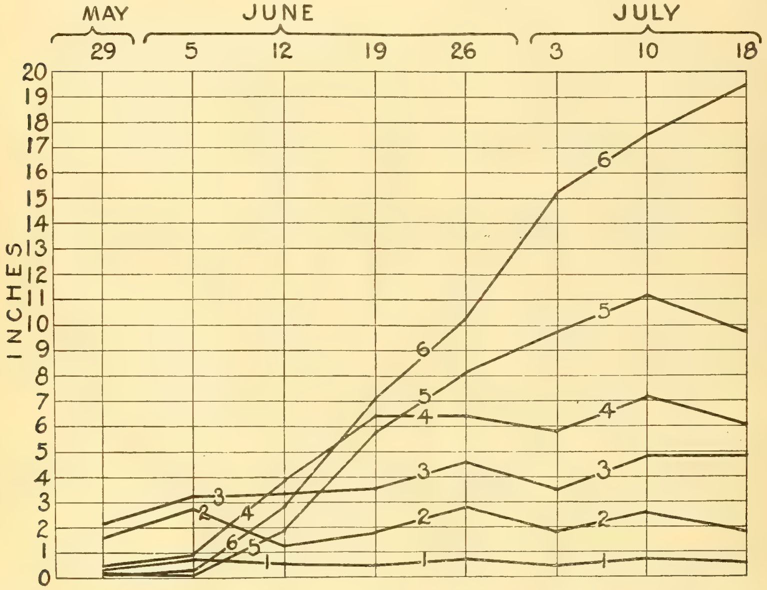


FIG. 3.—Curves showing relative growth of elongated internodes of timothy shoots. These curves are based on data presented in Table 4. Curve No. 1 represents the lowest elongated internode; No. 2, the next one above it, etc.

On each one of 33, or on 41.25 per cent of the 80 shoots of which measurements were made, there was one enlarged internode in the haplocorm and five internodes in the culm.

The lowest elongated internode of a timothy shoot is the first to develop, and those above it complete their growth in length, one after another, in progressive order, from the lowest to the uppermost. Table 4 and Figure 3 show that the lowest elongated internodes of the timothy shoots measured in 1916 made practically no increase in length after June 5, and the second and third internodes increased only slightly in length after that date. The combined length of the fifth and sixth elongated internodes on June 5 was less than that of any one of the four lower internodes. Later, when the lower internodes had ceased to increase in length, the fifth and sixth made their most rapid growth. The upper one continued to grow after each of the five internodes below it had attained its full length.

The manner in which the growth in length of the stems takes place, as well as some other phases of growth in the wheat plant (*Triticum aestivum* L.), very closely parallels the manner in which the same phases of growth occur in timothy (*28, p. 83*).

TWO TYPES OF TIMOTHY SHOOTS

That shoots of grasses may produce an inflorescence or be sterile has long been recognized by botanists (*13, p. 2; 31, p. 3*).

In addition to the fact that they do not produce inflorescences, sterile shoots differ from fertile ones in the following ways: (1) The stem of a sterile shoot is comparatively short and slender; (2) a sterile shoot may continue its growth during the late summer and fall, while on a fertile shoot all leaves become dry by the time the seeds mature in midsummer; (3) the number of elongated internodes and leaves on the culm of a sterile shoot becomes larger, in late summer or in fall, than on a fertile shoot.

A timothy plant with a number of shoots of each type is shown in Plate 5, *A*.

The relative proportions of fertile and sterile shoots in meadows vary widely under different conditions. In some meadows there are two or three times as many fertile shoots as there are sterile ones, while in other meadows the proportions are reversed; usually the relative proportions of the two types are more nearly equal.

FACTORS AFFECTING RELATIVE NUMBER AND PROPORTION OF EACH KIND OF SHOOT

The relative number and proportion of fertile or sterile shoots in any timothy meadow may depend upon one or more of several factors, all of which may be classed in two main groups.

(1) Cultural conditions. Some of the most important of these conditions are: (a) Age of the meadow; (b) available space in which the plants may develop; (c) quality of the soil.

(2) Hereditary tendencies of the plants of different varieties.

CULTURAL CONDITIONS

The results of some experiments described in the following paragraphs show that the number and proportion of fertile timothy shoots are larger in meadows where the cultural conditions are favorable for a vigorous growth than where conditions are less favorable.

Age of the meadow.—Two series of experiments have been conducted in broadcast plats of ordinary timothy, from which records were obtained in regard to the relative numbers and proportions of the two types of shoots in them from year to year as the plats became older.

The plats of one series were sown on the timothy-breeding field station at New London, Ohio, in September, 1911; the other plats were sown on the station at its new location at North Ridgeville, Ohio, in September, 1915. No fertilizers were applied on either series after they were sown. Typical square-yard areas were selected in each of four plats at New London and in each of three plats at North Ridgeville. The corners of these areas were marked so that records could be obtained from the same area in different seasons. Records were obtained at New London in the second, third, and fourth years when the plats produced hay crops; at North Ridgeville the records were obtained in the first and second seasons when hay crops were harvested.

The data obtained at New London are presented in the first part of Table 7 (records from the areas not fertilized); the data obtained at North Ridgeville are presented in Table 5.

TABLE 5.—*Average number and percentage of fertile and sterile timothy shoots and total number of shoots per square yard in three square-yard areas in two successive seasons as North Ridgeville, Ohio*

Items of comparison	Fertile shoots	Sterile shoots	Total
Number in 1916	530	381	911
Number in 1917	307	414	721
Percentage in 1916	58	42	----------
Percentage in 1917	43	57	----------

From the results obtained in these experiments, together with observations which have been made in other timothy meadows, the following conclusions have been derived:

> As meadows become older there is a general tendency for the number and also the percentage of fertile shoots per unit of area to become smaller from year to year. Varying seasonal conditions sometimes cause exceptions to this general rule.
>
> The number of sterile shoots per unit of area does not change so much as does the number of fertile shoots from year to year. The proportion of sterile shoots, however, is generally much larger in old than in new meadows, on account of the marked decrease in the number of fertile shoots.
>
> The total number of shoots, including both types, per unit of area tends to become somewhat less each year as meadows become older.

Available space for development.—An experiment was performed in 1916 in order to find out what the effect would be on the proportions of fertile and sterile shoots if a part of the plants growing in a meadow were removed so that the remaining ones would have more space in which to develop.

Two typical square-yard areas were selected in each of three broadcast plats of ordinary timothy, which were sown in September, 1915. On different dates from May 4 to May 13, 1916, a part of the plants were removed from one of the two square-yard areas in each plat; in the other area the plants were left to grow without being thinned (Table 6).

On July 10, 1916, the timothy was harvested and a record was obtained of the number of fertile shoots and of sterile shoots in each area.

TABLE 6.—*Effect of a thin and of a dense stand of plants in a timothy meadow on the proportion of fertile and sterile shoots*

Stand	Plat No.	Number of plants in square-yard area (counted May 4 to 13, 1916)	Percentage of shoots, July, 1916	
			Fertile	Sterile
Normal stand of plants	1	1,004	34	66
	2	991	42	58
	3	1,004	52	48
Average	------	1,000	43	57
Part of plants removed	1	325	46	54
	2	316	60	40
	3	383	66	34
Average	------	341	57	43

The data in Table 6 show that when part of the timothy plants were removed in the spring, so that the average number per square yard was reduced from 1,000 to 341, the result was that 57 per cent of the shoots in the thinned areas produced heads, while but 43 per cent of the total number of shoots in the areas where none of the plants were removed produced heads.

Additional information in regard to the relation of the space which is available to timothy plants for development to the proportion of fertile and sterile shoots was obtained in 1916 from records of the number of shoots of each type in a row plat of ordinary timothy. The rows in the series of plats in which these plants were growing were 3.3 feet apart, and the plants were 2.5 feet apart in the rows. On the 22 plants in this row plat there were 681 fertile shoots (99.4 per cent) and only 4 (0.6 per cent) shoots were sterile.

The evidence which has been presented shows clearly that when timothy plants have ample space for growth, heads develop on a larger proportion of the shoots than when the plants are growing under more crowded conditions.

Effect of fertilizers.—In four broadcast plats of ordinary timothy seeded in September, 1911, duplicate square-yard areas were marked with stakes in 1913. One area was located in the east half and the other in the west half of each plat.

TABLE 7.—*Effect of fertilizers on the number and percentage of fertile and sterile timothy shoots per square yard area; average results from four areas not fertilized and from four fertilized areas*

Items of comparison	Number of shoots			Percentage of shoots	
	Fertile	Sterile	Total	Fertile	Sterile
Areas not fertilized:					
1913	242	689	931	26	74
1914	253	585	838	30	70
1915	88	484	572	15	85
Areas fertilized in the spring of 1914:					
1913	306	629	935	33	67
1914	507	470	977	52	48
1915	118	472	590	20	80

In the spring of 1914 an application of commercial fertilizer was made on one-half of each broadcast plat; on April 22 a 1–8–2 grade of fertilizer was applied at the rate of 640 pounds to the acre; on May 19 a mixture composed of equal parts of sodium nitrate and of the 1–8–2 grade of fertilizer was applied at the rate of 200 pounds to the acre. No fertilizer was applied in 1913 or in 1915.

Records obtained from these square-yard areas in 1913, 1914, and 1915 are presented in Table 7.

Fertilizers applied on a timothy meadow in the spring of 1914 caused a very marked increase in the same season in the number and proportion of fertile shoots per unit of area. The number of sterile shoots was somewhat less and the proportion much less in 1914 on the fertilized than on the unfertilized areas. The total number of shoots per unit of area was increased by the application of fertilizers.

VARIETAL DIFFERENCES

In the summer of 1916 the shoots were collected from typical duplicate square-yard areas in broadcast plats of 14 F. C. I. selections of timothy.[4] Duplicate samples were also collected from each of four plats of ordinary timothy. These plats were all located in the same series, and had been sown at the same rate, and grown under the same cultural conditions. The seed of each F. C. I. selection sown in these plats originated two or three generations earlier from a single plant. The ordinary timothy was grown from commercial seed.

In the plats of most of these selections there were no marked variations in the proportion of fertile and sterile shoots. In 3 of the 14 plats of selections, however, very marked variations, which are shown in Table 8 and illustrated in Plate 5, *B*, were found. In the plats of Nos. 3913 and 3937 there was a much larger number of sterile shoots per square yard than in plats of ordinary timothy. In the plat of No. 4096 the number of sterile shoots per square yard was much less than in either of the two selections already mentioned or in the plats of ordinary timothy.

TABLE 8.—*Average number per square yard and percentage of fertile and sterile timothy shoots in duplicate square-yard areas in each of four plats of ordinary timothy and in single plats of F. C. I. Nos. 3913, 3937, and 4096, from data obtained in 1916*

Variety	Number of shoots per square yard			Percentage of shoots	
	Fertile	Sterile	Total	Fertile	Sterile
Ordinary	460	516	976	47	53
No. 3913	401	959	1,360	29	71
No. 3937	398	947	1,345	30	70
No. 4096	415	125	540	77	23

The tendency to produce large numbers and proportions of short, leafy, sterile shoots has been found in F. C. I. No. 3937 in each one

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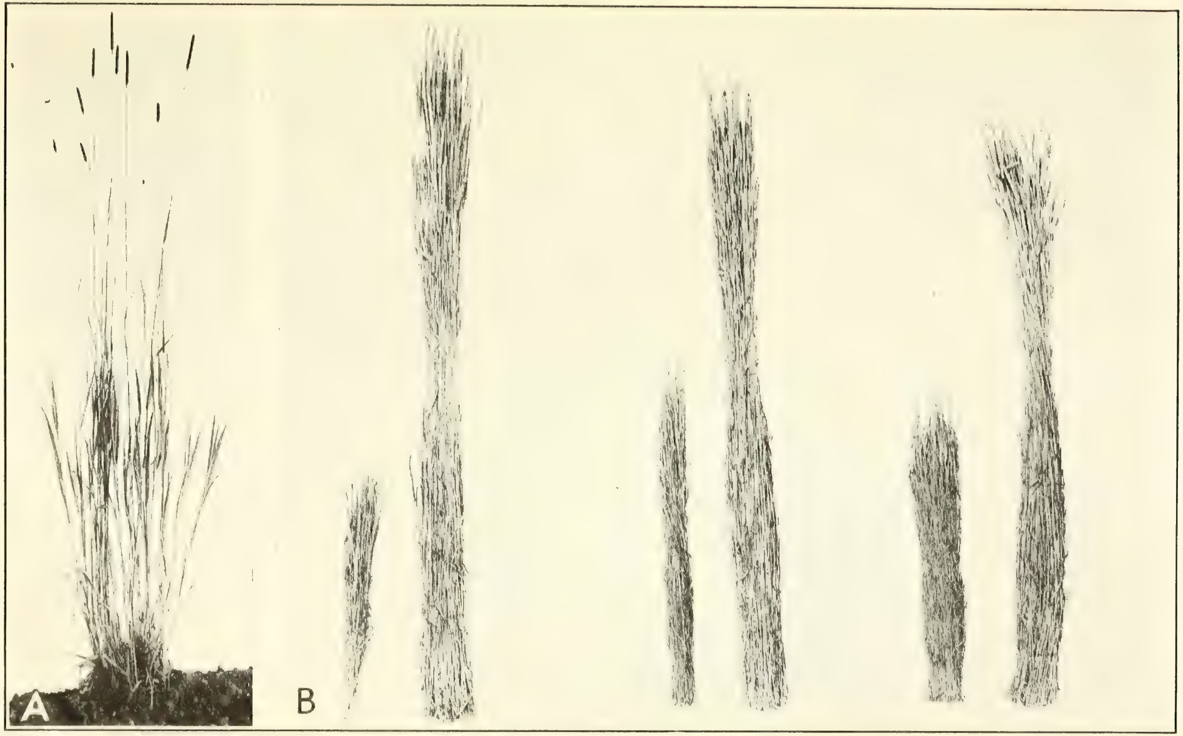
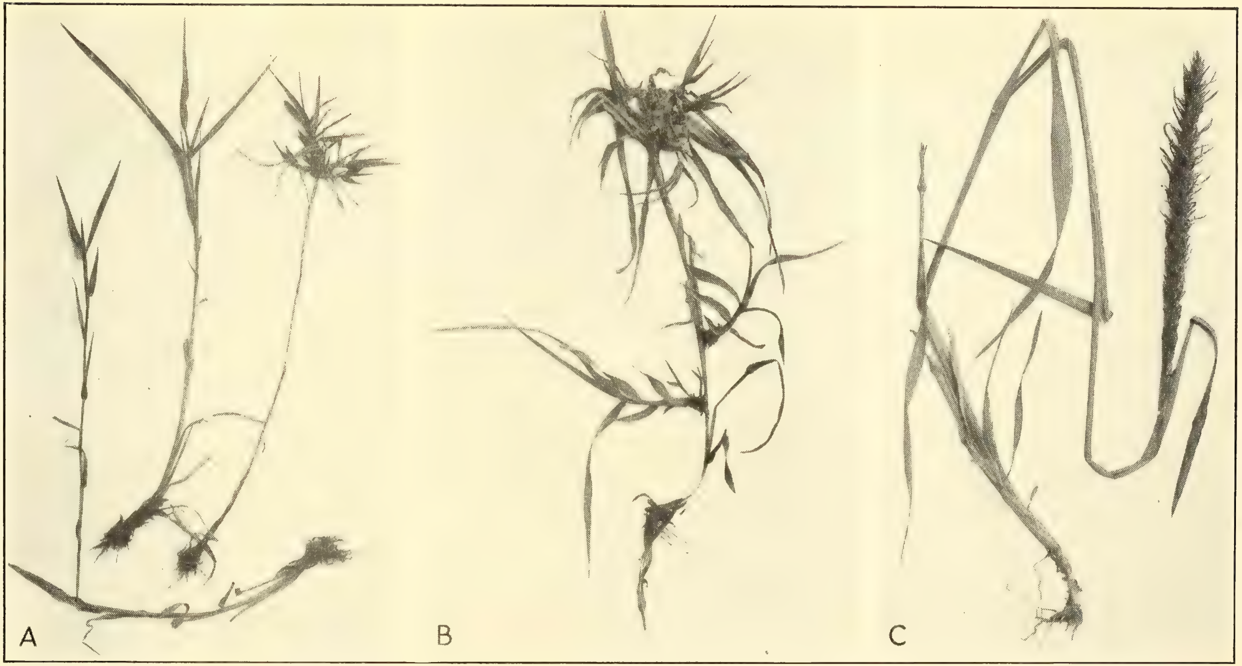
[4] The F. C. I. numbers referred to are in a series used by the Office of Forage Crops of the Bureau of Plant Industry, United States Department of Agriculture, for selections of timothy and other forage plants.



TIMOTHY PLANT AND SHOOTS

A.—A timothy plant from a 2-year-old meadow. There are 10 stems with heads and 19 stems without heads. On plants growing in very dense stands the number of stems of both types is usually less than on this plant. On July 29, 1922, when the photograph was taken, the leaf blades on some of the stems with heads were all dry; on each of the stems without a head there were several green leaf blades

B.—Shoots with and without heads, collected from 1 square yard in a broadcast plat of F. C. I. No. 4096 (left), of ordinary timothy (middle), and of F. C. I. No. 3937 (right). No. 4096 produced a relatively small and No. 3937 a relatively large proportion of sterile shoots



VARIATIONS IN TIMOTHY SHOOTS

A.—Typical timothy shoots without heads, late in the growing season (Nov. 7, 1914). On each shoot the lower leaves, which developed early in the season, were dry when the photograph was taken. The upper internodes of the middle shoot and of the shoot at the right are not elongated. In the latter shoot several small innovations have developed from buds in axils of leaves at the tip

B.—A shoot with young branch shoots or innovations growing at nodes between elongated internodes. Innovations which develop on the upper part of sterile shoots in the autumn usually grow only from nodes at the tip between nonelongated internodes

C.—A timothy shoot bearing a head with proliferating florets. The base of the head is partially inclosed in the upper leaf sheath of the culm; this condition is quite characteristic. More leaves are growing from the culm of this shoot than on the culms of typical shoots with heads which develop in midsummer of the seasons when this characteristic of it has been studied. In some plats of ordinary timothy from which records were obtained in each of the four years from 1916 to 1919 there was an average total number of 759 shoots per square yard, whereas in plats of No. 3937 grown under the same conditions there were 1,033 shoots per square yard. In the plats of ordinary timothy 44 per cent of these shoots were fertile, whereas in the plats of No. 3937 there were only 24 per cent of fertile shoots and a correspondingly larger percentage of sterile shoots than in the plats of ordinary timothy.

It is evident from these records that there is an inherent tendency in some varieties of timothy to produce fertile shoots and sterile shoots in numbers and proportions different from those of other varieties.

DESCRIPTION OF FERTILE SHOOTS

At the base of all timothy shoots is the short proaxis; next to it the haplocorm develops, and above this is the culm. A timothy shoot bearing a head is terminated by it.

The different parts composing a timothy shoot bearing a head and the divisions of the stem are described in the accompanying diagram. The relative position of the parts of the stem is also shown graphically in Figure 4.

Shoot
- Stem (axis)
  - Proaxis
  - Haplocorm
  - Culm
  - Rachis
- Roots
- Leaves
- Buds
- Inflorescence (head)

THE PROAXIS[5]

The fertile timothy shoot, illustrated diagrammatically in Figure 5, developed from a bud at the base of a shoot of the preceding year's growth. The proaxis is included between the points *a* and *b*. It is ordinarily composed of 10 to 15 or more nodes and nonelongated internodes, with a leaf at each node. By the time that a shoot has produced a head these basal leaves have become dry. It is from the nodes of the proaxis that the roots grow. In the axil of each leaf is a bud which may grow into a shoot when conditions become favorable. The leaves and buds grow alternately in two ranks on the proaxis just as they do on the upper part of the stem. A typical proaxis is illustrated in Figure 6.

The proaxis makes its growth between the time when the shoot first develops from a seed or bud, usually in late summer or early autumn, and about the 1st of the following May. The haplocorm and culm, as has already been stated, make their growth after this time[6] (*25, p. 61–65*). The length of the proaxis on 10 typical shoots collected from a 2-year-old meadow on June 3, 1914, varied from 0.22 to 0.56 inch in length; the average length was approximately 0.375 inch.

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[5] C. V. Piper suggested the term proaxis for the basal part of the stem of grasses.

[6] EVANS, M. W. THE LIFE HISTORY OF TIMOTHY. George Washington University thesis, p. 31–38. 1920. Unpublished.

NUMBER OF INTERNODES PER SHOOT

A series of experiments was conducted for the purpose of determining whether the number of internodes of timothy shoots is relatively constant or whether it varies to any marked degree.

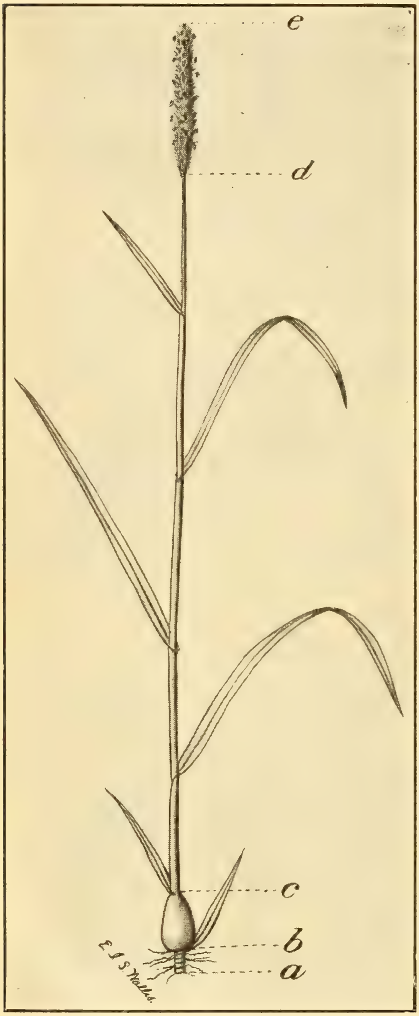


FIG. 4.—Diagrammatic drawing of a timothy shoot bearing a head. The relative positions of the parts composing the stem or axis are indicated. *a* to *b*, Proaxis; *b* to *c*, haplocorm; *c* to *d*, culm; *d* to *e*, rachis (the axis of the inflorescence)

In order to get data for the solution of this problem, shoots were selected on different plants and records were obtained from them in the following manner: Each shoot was examined early enough so that an accurate count could be made of all leaves, including the coleophyll on seedlings and the prophyllum of lateral shoots on older plants. One of the growing leaves on each plant was marked with insoluble ink and a record was made of its position. The shoot was observed at intervals, and a new leaf was occasionally marked. Since there is an internode above the node from which each leaf grows, if a record is obtained of the number of leaves which develop on a shoot, then the number of internodes can also be determined.

Each one of the shoots for which a record is presented in Table 9 produced a head on which florets bloomed and seeds formed during June and July.

Six groups of shoots were studied. These groups are arranged in two classes. In the first class of groups, A–1 to A–3, inclusive, the shoots grew directly from seeds. In the second class of groups, B–1 to B–3, each shoot developed from a bud in the axil of a leaf of an older shoot.

The cultural conditions under which the plants of each group were grown are described below:

Group A–1.—These shoots were grown from seeds sown in a broadcast plat on September 13, 1918.

Group A–2.—Seeds were sown in a box of soil about March 1, 1916. The box was kept in a warm room and the soil was watered at intervals until

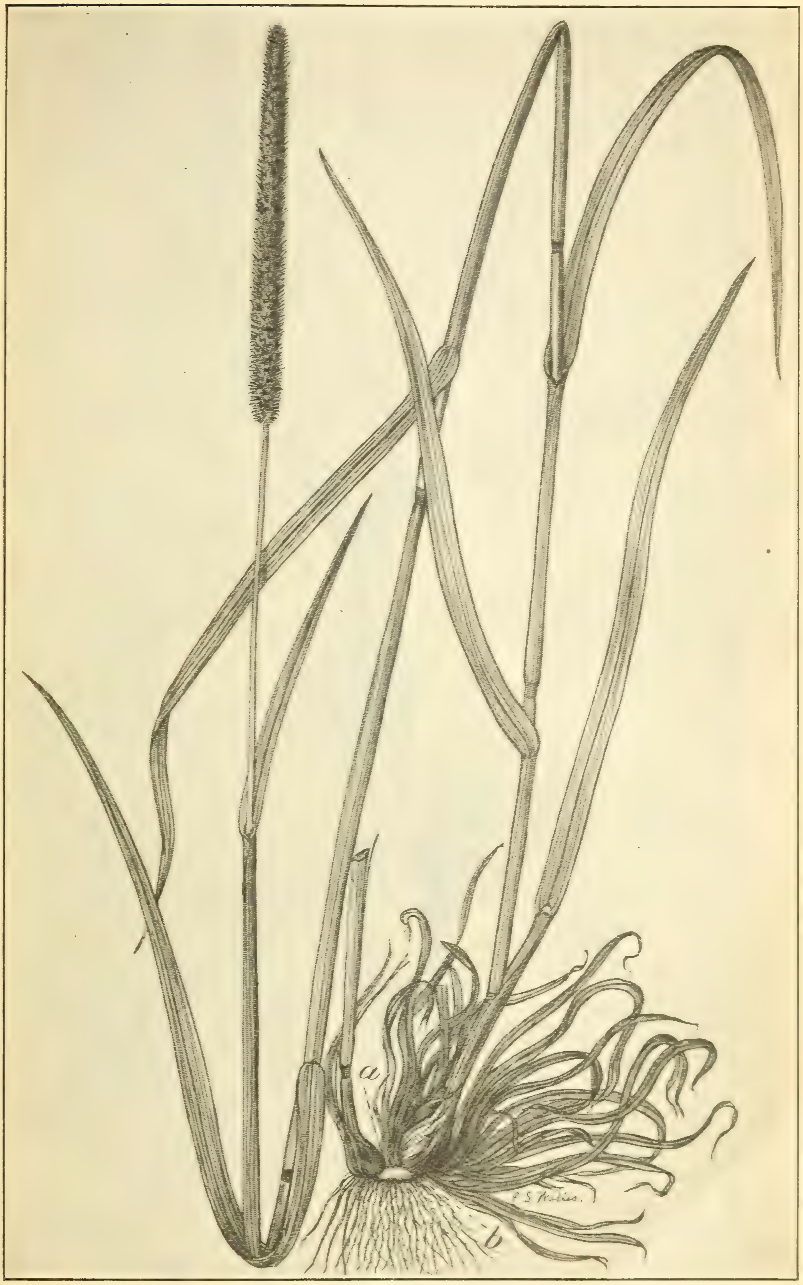


Fig. 5.—A timothy shoot with head. The proaxis, from the nodes of which the roots grow, extends from *a* to *b*. The dry parts of leaves ordinarily hide the proaxis from view, but in this drawing it is shown with no covering of leaves in order to illustrate it more clearly. The stubble of the parent shoot from which the growing shoot originated is also shown

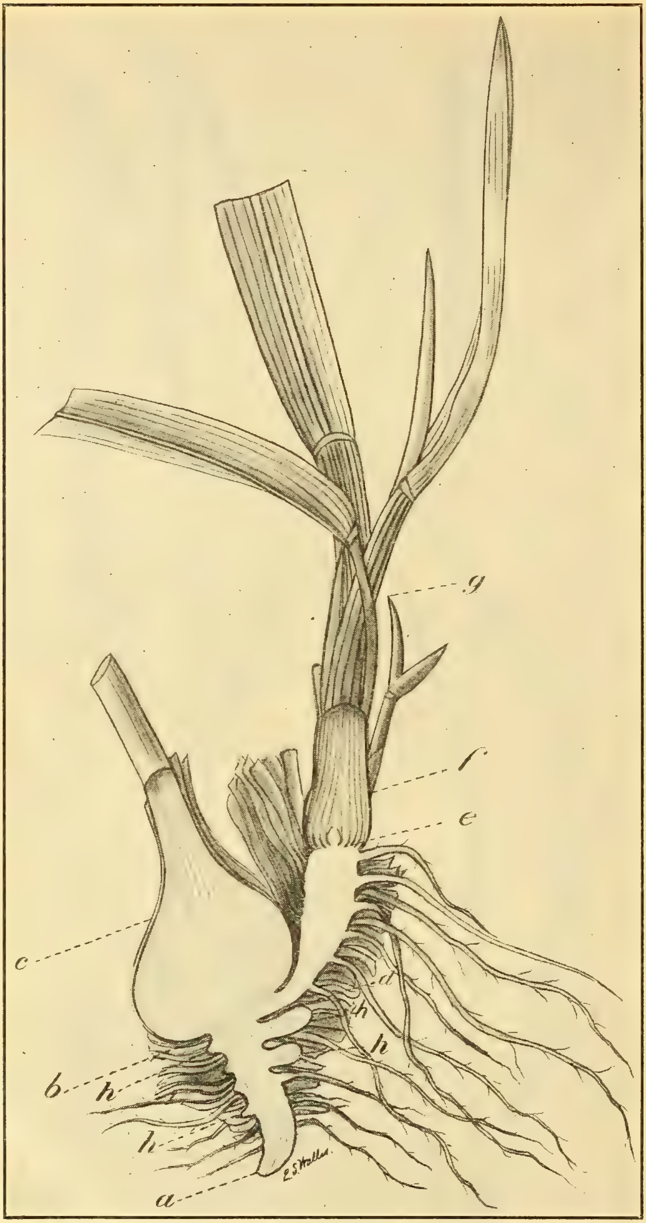


FIG. 6.—The proaxis (*d* to *e*) of a branch shoot which developed several months earlier from a bud in the upper part of the proaxis (*a* to *b*) of the primary shoot. The haplocorm of the primary shoot extends from *b* to *c;* that of the lateral shoot has not yet developed. There are several buds (*h*) which did not develop into branches on the proaxis of the primary shoot. No buds are visible in this view of the proaxis of the branch, since they are located in a plane at right angles to those on the primary shoot, though the upper part (*f* to *g*) of a small shoot grown from a bud on the branch from the primary shoot is shown. The terminal bud of the lateral shoot is shown at *e*

early in April, when the plants were transplanted to a field plat. There were several leaves on each plant at the time it was transferred to the field.

Group A–3.—Seeds were sown in a field plat early in April, 1916.

Group B–1.—The plants in this group were growing in a broadcast plat of timothy which had been sown in September, 1915. On December 10, 1918, a number of vigorous shoots with a comparatively large number of leaves, all of which were intact at that date, were selected for further observation. Since from 15 to 20 leaves had developed by December 10 on each one of the shoots included in this group, it is evident that these shoots must have developed from buds some time in the summer of 1918.

Group B–2.—The plants in this group were growing in an old timothy meadow. The shoots were first observed November 11, 1915. On one shoot there were four and on the other there were five leaves in addition to the prophyllum. Apparently these shoots had grown from buds comparatively late in the season of 1915.

Group B–3.—The plants used in this experiment were making a vigorous growth in cultivated row plats. On May 11, 1916, shoots on which there were from two to seven leaves were selected for observation. From the small number of leaves on each one of these shoots it is apparent that most, if not all, of them had developed from buds in the spring of 1916.

The records of all shoots which were used in this experiment are presented in Table 9.

TABLE 9.—*Effect of length of the growing period on number of internodes in timothy shoots collected for study in the July following the time when they developed from seeds or buds*

Growth of shoots	Number of shoots observed	Length of stems (inches)	Average number of internodes		
			Total	In pro-axis	In haplocorm and culm
Shoots grown from seed:					
Group A–1; seed sown in September	5	39. 5	21. 0	14. 6	6. 4
Group A–2; seed sown approximately March 1	8	38. 1	17. 2	11. 7	5. 5
Group A–3; seed sown in April	8	33. 4	12. 3	7. 0	5. 3
Shoots grown from vegetative buds:					
Group B–1; shoots developed from buds in summer	3	38. 3	28. 3	21. 3	7. 0
Group B–2; shoots developed from buds in autumn	2	38. 0	18. 0	12. 0	6. 0
Group B–3; shoots developed from buds in spring	7	38. 9	10. 1	4. 3	5. 8

The following conclusions are evident from the data which have been presented:

The number of internodes sometimes varies to a great extent.

There is a relatively small amount of variation in the number of internodes per shoot in those shoots which have developed during the same growing period and under approximately the same cultural conditions. Thus, in Group A–1 the range in the total number of internodes per shoot was from 20 to 23; the total number of internodes per shoot ranged from 15 to 19 in Group A–2, and from 11 to 14 in Group A–3.

The total number of internodes per shoot in a general way varies directly according to the length of the growing period. This is illustrated by the records of the shoots on the plants in Groups A–1 and A–3. The plants in the former group were from seeds sown in September, and the plants in the latter group were grown from seeds sown early in April. On the shoots from seeds sown in September there was by the following July an average total number of 21 internodes per shoot; on the shoots from seeds sown in April there was an average total number of 12.3 internodes per shoot.

VARIATION IN NUMBERS OF NONELONGATED AND ELONGATED INTERNODES

The greatest variation in the numbers of internodes in shoots which have developed during growing periods of different lengths occurs in the proaxis. The data in Table 9 show that in shoots grown from seeds sown in September there was an average of 14.6 nonelongated internodes, whereas in shoots grown from seeds which were not sown until April there was an average of only 7 internodes in the proaxis.

Table 9 shows that there is also some variation in the number of internodes in the elongated part of shoots which have had different growing periods, though this variation is very much less than in the number of nonelongated internodes. The shoots from seeds sown in September had an average of 6.4, while the shoots from seeds sown in April had an average of 5.3 elongated internodes in the haplocorm and culm.

On July 15, 1916, 30 fertile shoots were taken at random from a meadow of ordinary timothy. The number of elongated internodes in these shoots is shown in Table 10.

TABLE 10.—*Number of elongated internodes per shoot in 30 fertile shoots collected from an ordinary meadow on July 15, 1916*

Items of comparison	Number of elongated internodes		
	Haplocorm	Culm	Total
19 shoots (63.3 per cent) had	1	5	6
5 shoots (16.6 per cent) had	2	5	7
4 shoots (13.3 per cent) had	1	4	5
1 shoot (3.3 per cent) had	1	6	7
1 shoot (3.3 per cent) had	2	6	8

The number of elongated internodes in the timothy shoots collected on July 15, 1916, varied from five to eight. The average number of elongated internodes per shoot was 6.1. Similar records which have been obtained at different times show that the results presented in Table 10 are fairly typical of records that might be obtained in any ordinary timothy meadow.

Fertile shoots having more than seven or eight elongated internodes are comparatively rare among those which develop in early summer. In the aftermath which grows during midsummer and autumn fertile shoots having eight or nine or more elongated internodes are common. These fertile shoots having supernumerary elongated internodes are often relatively short. Shoots of this kind, like the fourth and fifth stems from the left in Plate 4, *B*, may perhaps be regarded as gradations between typical fertile shoots and typical sterile ones.

RELATIVE LENGTH OF DIFFERENT ELONGATED INTERNODES

The lowest elongated internode of a normal fertile timothy shoot is the shortest, and each succeeding internode has a greater length than the one below it (*26, p. 135–137*). This is illustrated by the record in Table 11 of the average lengths of the internodes of eight fertile timothy shoots collected from a meadow on July 15, 1916. Each shoot had one enlarged internode in the haplocorm and five elongated internodes in the culm. The internodes are numbered in order from the lowest to the highest. The average length of the heads on these shoots was 3.76 inches. The average length of the shoots, including the heads, was 51.63 inches.

TABLE 11.—*Average length of elongated internodes of eight fertile timothy shoots collected July 15, 1916*

Item	Internode No.	Length
		Inches
Haplocorm	1	0.67
Culm	2	2.50
	3	5.27
	4	8.01
	5	11.73
	6	19.67

LENGTH OF FERTILE TIMOTHY SHOOTS

The ordinary lengths of fertile timothy shoots growing under different conditions are indicated by the data presented in the following paragraphs. Although fertile shoots are frequently found which are less than 30 inches in length, and although they are sometimes 60 inches or more long, the more usual range in length is from about 36 to 48 inches.

Shoots of plants growing in a productive soil become longer than on plants growing on a poorer soil. They are likely to grow to a greater length in new than in older meadows. The lengths of the shoots in several timothy meadows of different ages were measured on August 6, 1917. In one meadow sown and fertilized in the preceding September most of the shoots measured from the base to the tip of head ranged from 42 to 48 inches in length; the average length was about 45 inches. A small proportion of the shoots in this meadow were 50 inches or more in length. There were also some shorter shoots, not over 30 or 33 inches in length, each with a comparatively small head. In a meadow in an adjoining field in which the second season's crop of timothy was growing the average length of the shoots was about 42 inches. In another near-by meadow, 3 years old or more, the average length of the shoots was about 40 inches.

The length of the shoots is determined not only by the cultural conditions under which the plant has been grown, but also by hereditary tendencies. In August, 1917, the length of the longest shoot of each one of the plants growing 2.5 feet apart in two cultivated row plats, each of which was 62.5 feet long, was measured. These rows were located parallel to each other, 3.2 rods apart, on uniform soil, and had received the same cultural treatment. The plants in one row had been propagated from the seeds of one original plant, and the plants in the second row from the seeds of another original plant. In the first row the lengths of the longest shoots of the different plants ranged from 38.5 to 47 inches; the average length was 42.9 inches. In the second row the longest shoots of the different plants varied from 44 to 55.5 inches in length, and the average length was 51.8 inches, or 8.9 inches more than the average length of the longest shoot of the different plants in the first row.

DESCRIPTION OF STERILE SHOOTS

The differences between timothy shoots which produce an inflorescence and those which are sterile have already been outlined. In the following paragraphs the more important of these differences are discussed more fully. Typical sterile shoots as they appear in midsummer are shown at the left in Plate 4, *B*.

STERILE SHOOTS ARE RELATIVELY SHORT

One of the most conspicuous of the distinctions between fertile and sterile shoots is that those of the latter type are shorter and also more slender than fertile shoots. In one meadow in which the average fertile shoot growing in a typical area measured 38.1 inches in length, it was found that the lengths of the sterile shoots growing in the same area varied from 7.5 to 22.5 inches and their average length was 14.4 inches.

STERILE SHOOTS HAVE RELATIVELY LARGE NUMBERS OF ELONGATED INTERNODES

Another one of the characteristics which distinguish sterile timothy shoots is the greater number of elongated internodes and leaves than on fertile shoots.

On July 20, 1912, and again on July 20, 1916, 10 typical shoots of each type were selected from a meadow and a count was made of the internodes and leaves on the elongated part of each. On July 20, 1912, on the fertile shoots there was an average number of 6.4 elongated internodes and on the sterile shoots 8.4 elongated internodes; on July 20, 1916, there was an average number of 6.9 elongated internodes on the fertile shoots and 8.5 elongated internodes on the sterile shoots.

As the season progresses the number of leaves on sterile shoots continues to increase as long as they remain green and continue growth. On 10 shoots of this type which were collected on December 12, 1918, the average number of leaves which had developed from the leaf below the haplocorm to the one at the tip of each stem was 17.3.

GROWTH OF STERILE SHOOTS MAY CONTINUE INDEFINITELY

Though the growth of new leaves from a fertile shoot ceases when the inflorescence develops, leaves continue to form on sterile timothy shoots until growth is checked by cold weather in late fall or early winter, unless the shoots dry up or are destroyed in some other way during late summer or early fall. This habit of growth is one of the most prominent of the characteristics of sterile shoots.

That the growth of a sterile shoot may continue through more than one season is shown by the results of two experiments described below.

A timothy plant having a sterile shoot was taken from the field late in November and transferred to a greenhouse December 18, 1918. The shoot was bent over and the tip partly covered with soil. On January 7, 1919, it was found that roots had developed from the covered nodes at the tip of the shoot and the new leaves were making a vigorous growth. The elongated internodes which developed in

1919 were separated from those which had developed on the same axis in the spring and summer of 1918 by a number of nonelongated internodes. The length of the elongated part of the shoot which grew in 1918 was 16.2 inches; the length of that which grew in 1919 was 7.9 inches. Seventeen leaves, counting the leaf which grew from the base of the haplocorm, developed prior to December 12, 1918, and 13 leaves developed after that date during the winter and spring of 1919, making a total number of 30 leaves during two seasons' growth, in addition to leaves which grew on the proaxis before the culm began to develop in the spring of 1918. At the time when this plant dried up in the greenhouse in the spring of 1919 no head had appeared on the shoot under observation.

Another sterile shoot with its tip partly covered with soil in a greenhouse bench to which the plant had been transplanted November 3, 1916, continued its growth through the following winter, spring, and early summer. A head on which florets in bloom were observed on July 7, 1917, terminated the growth of this shoot.

CHANGES IN STERILE SHOOTS DURING LATE SUMMER AND FALL

During late spring and early summer the internodes of sterile shoots become elongated in the same way as on fertile shoots, except that the elongated internodes do not attain as great length as on a shoot producing a head. During the latter part of the summer, however, the new internodes which develop at the tips of sterile shoots are progressively shorter. The internodes which develop later in the fall are not elongated, and the leaves at the tips of these shoots grow close together in much the same way as on the proaxis (*13, p. 4–5*).

On the 10 sterile shoots referred to in a preceding paragraph, which were collected on December 12, 1918, counting from the leaf at the node below the haplocorm to the most recently developed leaf on the shoot, there was an average number of 17.3 leaves; yet there was an average of only 10.8 elongated internodes per shoot. This shows that there was an average number of 6.5 leaves near the tips of these shoots growing from nodes not separated by elongated internodes. In this nonelongated terminal part of these shoots during the fall months buds and innovations frequently develop in the leaf axils.

The blades of the leaves at the tip of sterile shoots in the fall months are usually shorter than the blades of leaves which develop during late spring or early summer.

Typical short leafy sterile shoots as they appear in the fall are shown in Plate 6, *A*.

Occasionally lateral shoots or innovations develop from nodes between elongated internodes of sterile shoots. One of these shoots found on November 6, 1914, is shown in Plate 6, *B*. This condition is very uncommon in plants of ordinary American timothy.

It has been suggested that innovations at the tips of sterile shoots are one of the provisions of nature by which timothy plants reproduce themselves (*23, p. 145*). When a shoot of this type is artificially bent over and the base of the innovation at its tip is covered with moist soil, the innovation readily produces roots and becomes an independent plant. Only once during the course of these investigations has a sterile timothy shoot on a plant growing in a meadow been observed to become naturally bent over so that one or more of the innovations at its tip had come into contact with the soil and produced roots. In some semiprocumbent European forms of *Phleum pratense* or allied species, however, the stems frequently become rooted at nodes in the culm (*43, p. 155*). It may be concluded, therefore, that while timothy plants do sometimes reproduce themselves by means of innovations growing at the tips of sterile shoots, yet this method of reproduction is not a common one in timothy plants of the types which commonly grow in meadows in America.

The habit of vegetative reproduction at the tips of sterile shoots is not peculiar to timothy, though it has not been found in all perennial grasses which have been observed. In a plat of redtop (*Agrostis alba* L.) on the timothy-breeding field station in the fall of 1919, buds and innovations were growing in the axils of leaves near the tip on a considerably larger proportion of the sterile shoots than in the near-by plats of timothy. On the other hand, in plats of tall oat grass (*Arrhenatherum elatius* L.) and brome grass (*Bromus inermis* Leyss.) observed in November, 1919, although sterile shoots were numerous, on none of them was a bud or an innovation found in the axil of a leaf near the tip.

RELATION OF THE TWO TYPES OF SHOOTS TO EACH OTHER

No indication has been found that the buds from which fertile lateral shoots develop have a position on the primary shoots different from that of the buds which develop into sterile shoots. Whether any shoot may produce an inflorescence or not depends upon the cultural conditions under which the plant is growing, rather than upon the position of the bud from which the shoot has grown.

One question which suggests itself in any study of fertile and sterile timothy shoots is whether either kind of shoot may originate from a bud at the base of a shoot of the other type. In order to get data which would answer this question, an experiment was conducted in 1916 in an old meadow which had not been mowed in 1915.

On different dates from May 19 to 24, 1916, 21 partially elongated shoots which had developed from buds at the base of shoots which produced heads in 1915 were marked and their later development observed. The plants were growing in a comparatively dense stand, under conditions which were fairly typical of any ordinary timothy meadow. Thirteen of the twenty-one shoots which were marked continued their growth until July; on each one of five, or 38.5 per cent, of these shoots a head was produced, and eight, or 61.5 per cent of the shoots were of the short, leafy type with no head.

On 10 other plants in the same meadow small lateral shoots growing from the base of shoots of the short, leafy type, which did not produce heads in 1915, were also marked at the same time for observation. After these plants had been selected the surrounding ones were removed, loose soil was placed about the plants, and a small quantity of 2–12–0 grade of commercial fertilizer was applied about them on May 25, 1916. Conditions during the remainder of the season were therefore favorable for a vigorous growth. Eleven of the twelve shoots marked on these plants continued growth until July. On 10, or 90.9 per cent, of them a head developed on each, while no head developed on the remaining shoot (9.1 per cent).

The results of this experiment show conclusively that either a fertile or a sterile timothy shoot may develop vegetatively from another shoot of either type.

ROOTS

The general appearance of the root system of timothy plants is illustrated in Plate 2, *A* and *B*.

There is usually one seminal root on a timothy seedling. The roots which develop later on the primary shoot and all roots on later shoots developed from buds on the plant grow from nodes, generally from the nodes of the proaxis. They are slender or fibrous. Some of the roots have numerous branches and subbranches, while on the same plants other roots may be found which have grown without the development of any branches, to a length as great as or greater than that of the branched roots.

DEPTH TO WHICH TIMOTHY ROOTS GROW

The roots of timothy plants, like those of other grasses, grow at relatively shallow depths (*41, p. 92–93*). Ten Eyck found that none of the roots of a timothy plant which he examined in North Dakota extended down to a depth of 3 feet. The roots of timothy did not grow to so great a depth as the roots of either native prairie grass or of brome grass (*32, p. 540*).

Woods studied the distribution of the roots at different depths in a timothy meadow located on a clay loam soil in Connecticut (*44, p. 29*). From the data which he obtained he calculated the air-dry weight of roots per acre in the first, second, third, and fourth 6-inch layers of soil to be as follows:

Weight of roots from the first (upper) 6-inch layer of soil, 2,170 pounds per acre; second layer, 274 pounds; third layer, 58 pounds; fourth layer, 14 pounds.

PERIOD DURING WHICH TIMOTHY ROOTS CONTINUE GROWTH

There is no evidence at hand to indicate how long a single timothy root may continue to live. It is not known whether the first roots which develop on a shoot continue to function until the upper part of the shoot becomes dry several months or a year later or whether each root lives for a more limited period of time.

In a meadow which had been harvested in the preceding July or August the stubble of the shoots was examined October 22, 1914. At that time the haplocorms of practically all shoots were still green in color and firm in texture. At the node above the haplocorm of some of these shoots there was a bud which had expanded to form leaves, but which did not have any root system of its own. On the stubble of such shoots some of the roots were evidently continuing to function at that time.

The roots of the elongated shoot of any particular season's growth have been observed usually to appear brown and lifeless in the following spring. On March 19, 1914, the stubble of a shoot of the preceding season's growth, together with several attached innovations each with its own root system, was partially immersed in water.

On March 21 it was observed that the roots of the innovations were making new growth, but the roots of the shoot which grew in 1913 showed no signs of life.

From the observations which have been recorded it may be concluded that at least some of the roots of a timothy shoot may continue to grow or function for several weeks or months after the upper part of the shoot has become dry, but by the following spring the roots on these shoots have usually all become lifeless. Timothy roots, then, are not perennial. The period of the life of all the roots of a shoot usually extends through part of one season and through part or all of the following season. Less frequently, on shoots which develop from seeds or buds in the spring, the period of growth of the roots of a shoot, like that of the shoot itself, may be limited to a single season.

THE HAPLOCORM

At the base of most elongated timothy shoots one, less frequently two, and occasionally three of the lowest elongated internodes become enlarged, to form the haplocorm. Typical haplocorms are shown in Plate 7, *A* and *B*.

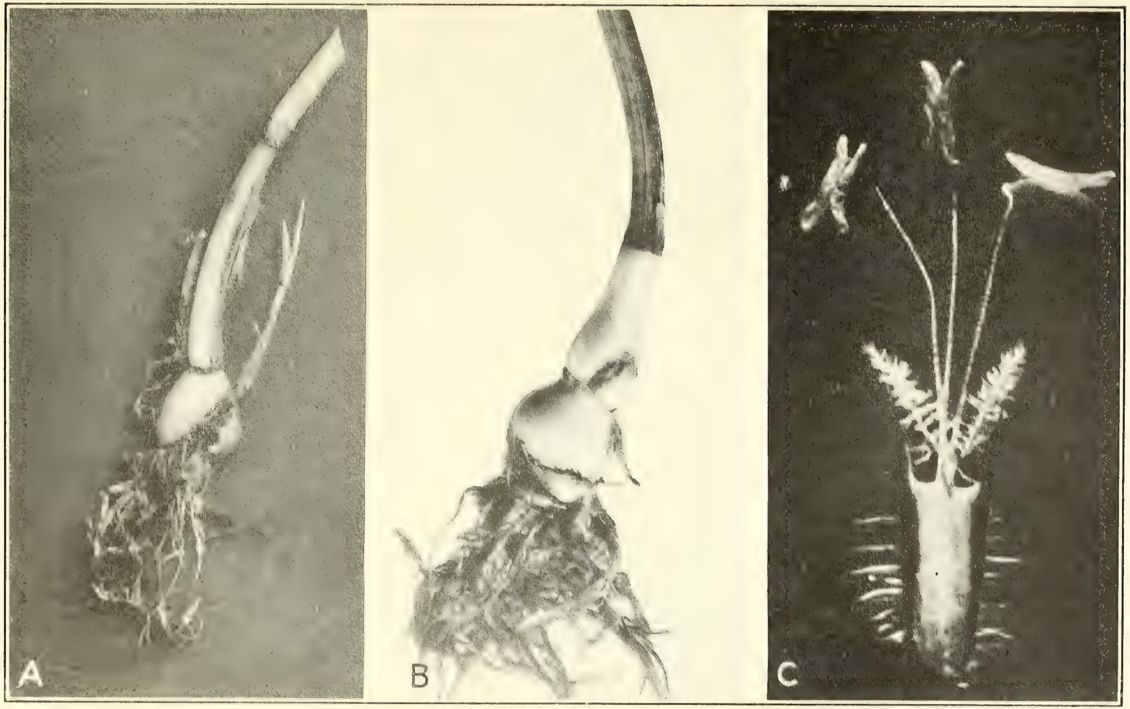
In one meadow which was examined in July, 1916, it was found that in a typical area of 1 square foot on 88.5 per cent of the elongated shoots the haplocorm was composed of a single internode, whereas on the other 11.5 per cent there were two enlarged internodes. In another meadow, examined in October, 1917, it was found that in a typical area 85.7 per cent of all stubble of culms had one enlarged internode, and on the remaining ones there were two enlarged internodes. Occasionally a shoot has been found with a haplocorm consisting of three enlarged internodes. However, as indicated by these records and by other data, usually 75 to 90 per cent of the haplocorms in any timothy meadow are composed of one and nearly all of the others are composed of two enlarged internodes.

A haplocorm is solid; in this respect, as well as in being shorter and having a greater diameter, it differs from the typical hollow cylindrical upper internodes of the culm.

In the spring of 1916 a series of measurements was made of a group of 16 timothy shoots, each with a haplocorm composed of a single enlarged internode, which ranged from 0.3 to 1.4 inches in length; the average length was 0.66 inch. When there are two enlarged basal internodes each one is usually shorter than on shoots with one enlarged internode, so that the length of the haplocorm usually is not greatly different, whether it is composed of one or two internodes.

The diameter, like the length of the haplocorm, varies in different timothy shoots; it is usually less than the length. The form of haplocorms also varies, as do the relative proportions of their lengths and diameters.

The fact that the haplocorm develops between nodes from which leaves have grown indicates that it grows above the surface of the soil; this is its normal position in shoots which have originated from buds on older shoots. Since the lower parts of timothy shoots often are more or less procumbent, the haplocorms grow in all positions

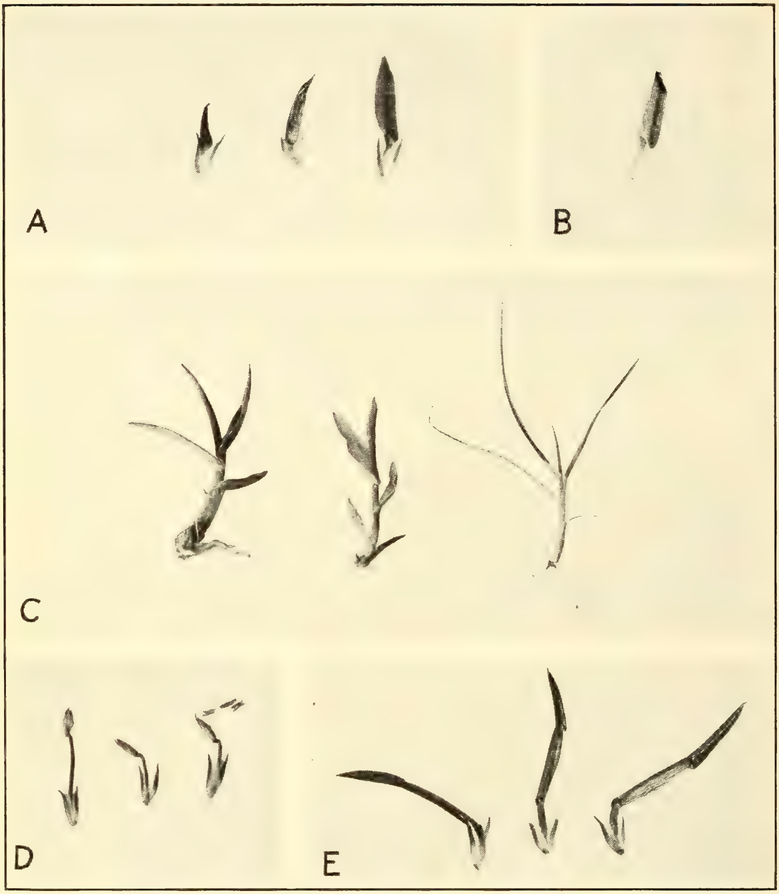


TIMOTHY HAPLOCORMS AND A SPIKELET

A.—A typical haplocorm composed of one enlarged internode at the base of a timothy shoot. A bud at the node above and another at one of the nodes below the haplocorm are expanding to form innovations

B.—A haplocorm composed of more than one enlarged internode. A bud is growing at a node between two of the enlarged internodes. At the base of the haplocorm there is another internode, only slightly elongated and enlarged. The leaves which were growing at the nodes have been removed

C.—A timothy spikelet with floret in bloom. (Much enlarged)



TIMOTHY SPIKELETS, FLORETS, AND SHOOTS

A.—Three timothy spikelets, each with one proliferating bract. (× 1.5)
B.—A proliferating timothy floret with a single enlarged bract. The empty glumes of the spikelet have been removed. (× 1.5)
C.—Young timothy shoots of three different kinds. The one at the right is the primary shoot of a seedling. The one at the left developed from an ordinary vegetative bud at the base of the stem of an older plant. The shoot at the center developed as a proliferation on a timothy head collected November 9, 1920. (Actual size)
D.—Timothy spikelets with elongated rachillæ. The glumes of the spikelets are in their normal position, while the parts of the florets are borne at the tips of the abnormally elongated axes. (× 1.4)
E.—Three proliferating timothy florets, each borne within the two unmodified empty glumes of the spikelet, at the tip of an elongated axis, which apparently is the rachilla. The lemma of each floret has been transformed into a leaf. This form of proliferation is rare in timothy. (× 1.5)

from vertical to horizontal and are commonly in close contact with the surface of the soil.

It was observed in 1917 in a new meadow which had been sown in September, 1916, that some of the haplocorms were partially and on a small proportion of the shoots were entirely below the surface of the soil. A considerable proportion of the shoots in this meadow had grown directly from seeds. When a timothy seed germinates at some distance below the surface of the soil, the base of the primary shoot and of the haplocorm which develops on it, instead of being entirely above the soil surface, as on the shoots of older plants, frequently is at a slight distance below it.

In some of the other species of Phleum there is usually an enlargement of the lower internodes of the shoots, which is apparently the same as the haplocorm of *P. pratense.* On shoots of *Melica geyeri* Munro there are enlargements of internodes at the bases which resemble the haplocorm of timothy. Different species of several other genera of grasses have enlargements or swellings of different kinds at the bases of the shoots (*14, p. 125–138; 18, p. 113*).

NAMES WHICH HAVE BEEN APPLIED TO THE HAPLOCORM

The enlarged basal internodes of timothy shoots have been designated in botanical and in agricultural literature by various names. The name which has been most commonly used is bulb (*37, p. 8; 38, p. 47–60*). The term tuber has also been applied to this part of the timothy shoot (*1, p. 76*). The name corm has sometimes been used (*1, p. 76*).

Neither of the names bulb or tuber used in its proper sense can be applied to the enlarged basal internodes of timothy shoots. A bulb is composed of the basal portions of leaves, which inclose a bud; the swelling at the basal part of a timothy shoot is composed of one or more internodes. A tuber is a part of an underground stem: the enlarged parts of timothy shoots normally grow above the surface of the soil.

A corm is defined by Jackson as follows (*21, p. 92*): "A bulblike fleshy stem or base of a stem; a 'solid' bulb." The swelling at the base of timothy shoots is a short, bulblike, fleshy part of the stem, but it differs from typical corms. The corm of a crocus or a gladiolus terminates in a bud, through which reproduction occurs: in timothy, vegetative reproduction occurs through buds in the axils of leaves, at nodes which may or may not be adjacent to the haplocorm. The roots of crocus or gladiolus grow from nodes at the base of the corm; on a timothy shoot the roots grow from the nodes of the proaxis. Crocus and gladiolus corms, which are generally regarded as resting organs in which nutrients have been stored, are composed of many short internodes; the enlargement at the base of a timothy shoot, the function of which has not yet been very clearly demonstrated, is most frequently composed of a single internode. The name corm, therefore, can hardly be properly applied to the enlargement at the base of timothy shoots.

Since no botanical term has been found which precisely describes the enlargement at the base of timothy shoots, the term haplocorm has been adopted.[7] The typical haplocorm of timothy, as the meaning of the term indicates, is composed of a single enlarged internode. The use of the term has been extended, so that it also applies to the swelling on the smaller proportion of timothy shoots composed of two or occasionally three enlarged basal internodes.

TIME WHEN THE HAPLOCORM MAKES ITS GROWTH

In a timothy meadow buds develop into young shoots or innovations in the largest numbers during the middle to the latter part of the summer. It is not until the following spring when the upper internodes of these shoots become elongated that the haplocorms are formed. The internodes of a timothy shoot develop in the same order of succession as the corresponding leaves appear. Since the haplocorm is the lowest one of the elongated internodes, it is the first one to develop. As it grows in length it also enlarges in diameter.

To some extent, in different seasons or in different latitudes, climatic conditions affect the time at which the haplocorms develop. At the timothy-breeding field station in northern Ohio a series of observations and measurements which were made from May 1 to July 31, 1916, showed that in that season the haplocorm of timothy shoots commenced to grow soon after May 1 and by June 5 their growth, both in length and diameter, was practically completed. At Washington, D. C., timothy shoots which were examined May 5, 1913, had well-formed haplocorms at that time, indicating that their growth must have begun some time in April.

At about the time, in midsummer, when seeds mature on a timothy shoot the leaves and upper internodes become dry. The lower part of the shoot, and especially the haplocorm, retains its green color for several weeks or months longer. In one meadow examined October 22, 1914, most of the haplocorms which developed in the preceding spring were still green in color and turgid in texture, although the stubble of most of the shoots had dried as far down as the node above the haplocorm. Records made on March 2 and April 3, 1914, of the condition of the haplocorms of shoots which developed in 1913 show that while most of the haplocorms retained their original form until the spring of 1914 their interior parts were more or less brown in color, were not turgid, and evidently contained no live tissue. The exterior part of the haplocorm is comparatively firm, and it frequently retains its form for a year or more after the inner tissue of the haplocorm has begun to decay.

CONDITIONS UNDER WHICH THE HAPLOCORM DEVELOPS

Haplocorms have been found commonly present on practically all timothy shoots which become elongated in late spring, whether the soil in which the plants have grown is or is not a very productive one. It has been observed, however, that the form of the haplocorm is sometimes apparently affected to some extent by soil conditions. On timothy plants growing in cultivated row plats the ratio of the diameter to the length is apparently less than in typical haplocorms from meadows where the plants are not making a very large or vigorous growth. There is no evidence, however, to indicate that the mass or volume of the average haplocorm is less on plants growing in cultivated row plats, or elsewhere where soil conditions cause a large and vigorous growth, than where the plants do not become so large (*10*, *p. 34*).

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[7] The name "haplocorm" was suggested by the late C. V. Piper. It is composed of the word "corm," which is derived from the Greek "kormos," and the prefix "haplo," from the Greek word "haplos," meaning single or simple.

Haplocorms are almost invariably present on shoots which have elongated during the latter part of spring, but they are sometimes absent, or not well developed, on shoots grown under different conditions. On October 22, 1917, in a timothy meadow where the first crop of shoots had been harvested in the July preceding, 20 shoots which had become elongated late in the season were examined. On each of 16, or 80 per cent, of these shoots there was a haplocorm, though its average size was somewhat less than is usual on shoots of the same size which elongate at the normal time in the spring. On 4, or 20 per cent, of these shoots there was no apparent enlargement in the diameters of the lowest elongated internodes.

Some of the early botanical writers classed timothy plants with haplocorms as *Phleum pratense nodosum*.[8] Instead, however, of being a character which can be used to distinguish a distinct subspecies, the haplocorm is commonly present on the shoots of plants of *P. pratense*.

RELATION OF THE HAPLOCORM TO VEGETATIVE REPRODUCTION

There is a potential bud in the axil of the leaf at each node adjacent to the haplocorm, but there is also a bud in the axils of other leaves.

It has been assumed by different writers who have discussed the growth of timothy that the development of the haplocorm is essential to the vegetative reproduction of the plant (*23*, *p. 94; 38*, *p. 47; 10*, *p. 303–306*). However, buds in the leaf axils of the primary shoot of a timothy seedling very commonly develop into vigorous secondary shoots, with independent root systems, before a haplocorm has formed on the plant. Plate 2, *A*, is an illustration of a timothy shoot on which there were several innovations making a vigorous growth, although no haplocorm had developed on the shoot. It is clear, therefore, that the timothy plant is not entirely dependent on the haplocorm to perpetuate itself through vegetative reproduction.

Whether the haplocorm may under other conditions have some effect on the growth of buds into shoots is not so clear. On plants in ordinary timothy meadows most of the buds remain dormant until about the time when the seeds mature, which is several weeks after the haplocorms have attained their full size. As has already been stated, the haplocorms continue to remain green and turgid for several weeks or months after the seeds have matured. It is during this period when the haplocorms are in their prime that large numbers of shoots on plants which grow in timothy meadows develop from buds. In a series of chemical analyses made at the Missouri Agricultural Experiment Station at six different intervals from the time when shoots of timothy plants were about 1 foot high until the seeds had matured, the haplocorms were found to contain less crude fiber and more material classed as nitrogen-free extract than did the parts of the shoots, including the leaves, which are above the haplocorm (*33, p. 49–50*). Although the haplocorm is not essential to vegetative reproduction of timothy, it may possibly serve to some extent as a storage of nutrients which are used by those innovations which grow from the buds at the base of elongated shoots during the summer months. It is also possible that some of the material stored in the haplocorm later becomes transferred to the seeds, which mature about 8 or 10 weeks after the haplocorm has completed its growth.

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[8] FRASER, S. TIMOTHY. Cornell University thesis, p. 75–80. 1905. Unpublished.

LEAVES

The leaves of timothy are composed of two main parts, the sheath and the linear blade, at the juncture of which there is a relatively short, broad, glabrous ligule. The size of timothy leaves in a general way corresponds to the size of the plant on which they grow. The leaves of a vigorous plant several months old are larger in both length and width than those of a plant only a few weeks old.

THE PROPHYLLUM

On innovations the first leaflike organ is short, with no blade; this is the prophyllum (*13, p. 5–6*). It grows with its back to the axis of the primary shoot, in the same plane as the leaves of the primary shoot, and in a plane at right angles to the plane in which the other leaves of the innovation grow.

THE LEAF SHEATHS AND BLADES

The first leaf above the prophyllum generally has a short, rudimentary blade, not exceeding 0.25 inch in length, though frequently no blade at all is developed. The second leaf above the prophyllum usually has a normal blade, though it also is sometimes short and rudimentary.

The sheaths of the leaves on a timothy shoot on which none of the internodes have become elongated are relatively short. The sheath of each leaf is inclosed within the sheath of the next older leaf. During the fall, winter, and early spring, up to the time when the upper internodes become elongated to form a culm, the growing bud of the shoot is inclosed within and near the base of the sheaths of all leaves which have developed on it (*17, p. 99*).

The sheath of each leaf is usually slightly longer than the sheath of the next older leaf. Thus, on five typical shoots which were collected from a timothy meadow October 29, 1917, the average length of the sheath of the first leaf above the prophyllum was 0.68 inch; of the second leaf, 0.95 inch; and of the third leaf, 0.99 inch. The sheaths of the leaves which develop in the spring, before the internodes begin to become elongated, have sometimes been found to grow to a length of 3 inches or more.

Like the corresponding internodes of the culm, the leaf sheaths are progressively longer toward the upper part of it. The lower internodes in the elongated part of the shoot are frequently entirely inclosed within the leaf sheaths. In the upper part of the culm the sheaths of the leaves are shorter than the corresponding internodes.

The length of the leaf blades on timothy shoots in early spring is less than the length of the blades which develop a few weeks later. This is illustrated by the following records of the average length, on different dates, of the green and partially green leaf blades on a typical shoot in the spring of 1914.

On April 18 the average length of all of the green leaf blades was 2.4 inches; on May 2 it was 2.4 inches; on May 16 it was 3.9 inches; and on May 29 it was 4.8 inches.

The blade of the upper leaf on the culm is usually shorter than the blades of the other leaves on it. This is shown by the results of measurements presented in Table 12, which were made in June, 1916, of the lengths of the sheaths and blades of the four upper leaves on five typical culms from a timothy meadow.

TABLE 12.—*Average length of sheaths and blades of the four upper leaves of five elongated timothy shoots*

Location	Average length (inches)	
	Sheath	Blade
Third from upper leaf	3.4	7.9
Second from upper leaf	4.0	8.5
Next to upper leaf	4.8	7.8
Upper leaf	6.4	3.4

THE NUMBER OF LEAVES ON TIMOTHY SHOOTS

Since one leaf grows at each node of a timothy shoot the number of leaves, nodes, and internodes of the shoot are the same. As has already been shown in Table 9, the total number of internodes and leaves which develop during the life of a shoot depends largely upon the length of its growing period. On the elongated part of fertile shoots there are usually five to seven, most frequently six leaves. On the elongated part of sterile shoots there are ordinarily more leaves than on fertile shoots, and the number of leaves on the former increases as long as they continue growth.

NUMBER OF LEAVES GROWING AT ONE TIME ON A TIMOTHY SHOOT

The leaves of timothy plants differ in their period of growth from the leaves of deciduous trees and shrubs. On the latter class of plants leaves unfold in the spring and remain green until the following autumn. On timothy plants leaves appear at any time and during the growing season each leaf remains green for a period of about two months or less. New leaves continue to appear in succession at comparatively regular intervals, then after remaining green during their usual period they become dry in the same order of succession in which they appeared.

The number of leaves with entirely or partially green blades on a timothy shoot at any particular time does not usually vary to any great extent from the time that the seedling or innovation has become fully developed until some time after the internodes of the shoot begin to become elongated. On most of the shoots for which records are presented in Table 13 there were either five or six green leaf blades; a few had four or seven; only one shoot had as many as eight leaves with green or partially green leaf blades.

TABLE 13.—*Number of leaves with entirely or partially green blades on different groups of nonelongated timothy shoots at different times during the growing season*

Date shoots were observed	Number of shoots from which records were obtained	Average number of leaves per shoot with entirely or partially green blades
Apr. 18, 1914	5	6.6
May 2, 1914	5	5.6
Aug. 30 to Sept. 1, 1916	24	5.7
Oct. 16, 1916	24	5.2
Nov. 7, 1916	4	5.5
Nov. 30, 1918	10	4.7
Dec. 7, 1918	5	5.6

Soon after June 1, when the internodes of the culms of fertile timothy shoots are making their most rapid growth in length, the number of green leaves begins to decrease. About the time when the seeds mature all of the leaves have become dry. The decrease in the amount of green-leaf tissue is actually somewhat more rapid than is indicated in Table 14, for the reason that the proportion of entirely green leaf blades to partially green leaf blades gradually diminishes. On the 14 shoots referred to in Table 14, on May 8, 80 per cent of the growing leaves had entirely green blades; on July 10 only 28 per cent of the growing leaves had blades entirely green.

On sterile shoots the leaf blades do not dry up nearly so rapidly as on fertile shoots. In one meadow examined August 5, 1922, it was found that on each one of the sterile shoots there were, as a rule, from three to five green leaf blades; whereas, in the same meadow on a large percentage of the fertile shoots there were no green leaf blades at that time. Although a considerable proportion of the sterile shoots in any meadow usually cease growth, especially if the weather becomes very dry, during the latter part of the summer, on many of them green leaves continue to develop until growth is terminated by cold weather in late autumn.

TABLE 14.—*Average number of leaves with blades entirely or partially green on 14 elongated fertile timothy shoots at intervals of one week during the spring and early summer of 1916*

Date observed	Average number of green leaf blades per shoot	Date observed	Average number of green leaf blades per shoot
May 8	6.7	June 26	3.9
May 15	6.0	July 5	3.2
May 23	6.0	July 10	2.6
June 5	6.2	July 17	1.7
June 12	5.5	July 24	1.0
June 19	4.9	July 31	0

HABITS OF GROWTH OF THE LEAVES

The first indication of a new timothy leaf is when the tip of the blade extends up from within the folded sheath of the next older leaf. As the blade grows it continues to emerge from within the leaf below it, and at the same time it gradually unfolds.

STAGE AT WHICH LEAF BLADES MAKE THEIR GROWTH IN LENGTH

A series of measurements was made of the blades of the three upper leaves of 14 elongated fertile timothy shoots. The data presented in Table 15 show that the blade of a timothy leaf has completed its growth in length by the time that it has emerged from within the sheath of the leaf below it.

Table 15.—*Average length of blades of timothy leaves at different stages of development*

State of blade	Leaf length (inches)		
	Second from upper	Next to upper	Upper
Just emerged	8.06	7.35	3.73
Tip beginning to become dry	8.13	7.43	3.69
Entire blade dry	8.10	7.41	3.69

PERIOD DURING WHICH TIMOTHY LEAVES REMAIN GREEN

After a timothy leaf has completed its growth it remains green for a time, then begins to dry gradually from the tip downward to the base of the blade, and then downward to the base of the sheath.

Records were made at intervals of three or four days during May, June, and July, 1916, of the time during which the blades of the same leaves referred to in Table 15 remained green or partially green. The data obtained are presented in Table 16. The total time during which the blades of the timothy leaves were entirely or partially green varied from about 50 to 60 days. Observations which have been made of other timothy leaves during the spring, summer, and fall indicate that in the growing season the usual period of time during which the blades of timothy leaves remain green is not greatly different from that indicated in Table 16.

Table 16.—*Average length of time during which timothy leaf blades were entirely or partially green*

Position of leaf	Days required for emergence of leaf blade[1]	Days from complete emergence until drying began at tip[2]	Days required for complete drying of leaf blade[3]	Days from appearance of tip until leaf blade was dry[4]
Second from upper leaf blade	12.5	25.3	20.5	58.3
Next to upper leaf blade	8.5	31.3	16.2	56.0
Upper leaf blade	4.3	33.2	12.8	50.3

[1] Average number of days from time when tip of leaf appeared until the blade had entirely emerged.
[2] Average number of days from time when leaf blade had emerged until it began to dry at the tip.
[3] Average number of days from time when leaf blade began to dry until it was entirely dry.
[4] Average total number of days from time when leaf blade first appeared until it was entirely dry.

On the other hand, it has been observed that during the winter months, when the plants are more or less dormant, leaves may remain green for a considerably longer time. On each one of 10 timothy shoots observed November 27, 1920, there was a partially opened leaf. On March 14, 1921, 107 days later, these same leaves were entirely open and each blade was nearly or entirely green. On another plant which was observed November 11, 1915, and again May 1, 1916, 172 days later, about one-half of the blade of a leaf which was partially unfolded on the former date was still green, though of a rather yellow-green color, when it was observed on the latter date.

FREQUENCY AT WHICH NEW LEAVES APPEAR

The frequency at which new leaves appeared on three groups of timothy shoots observed at different times in the growing season is shown in Table 17. The shoots in Group 1 were growing in the field from seeds sown September 20 and in Group 2 from seeds sown September 13. The shoots in Group 3 were growing on plants in an old meadow.

TABLE 17.—*Frequency at which new timothy leaves appeared on three different groups of shoots*

Group	Number of shoots in group	Period over which record extended	Length of period (days)	Average number of new leaves appearing per shoot	Frequency at which new leaves appeared (days)
No. 1	25	Sept. 20 to Oct. 30	40	3. 0	13. 3
No. 2	10	Sept. 13 to Dec. 9	87	6. 2	14. 0
No. 3	5	Apr. 18 to May 29	41	4. 2	9. 8

During May and June, 1916, on 14 other timothy shoots, which at that time were making a relatively rapid growth in length, the average time elapsing from the appearance of the third and that of the adjoining, next to the upper, leaf of the culm was 9.1 days. The average interval from the appearance of the next to the upper leaf and that of the upper leaf was 8.1 days.

On five timothy plants grown from January 5 to April 4, 1922, in a greenhouse where the temperature ranged from 48 to 60° F., an average interval of 8.7 days elapsed between the appearance of successive leaves on the shoots which were observed.

The records which have been presented show that during the growing season a new timothy leaf appears on timothy shoots about once every 8 to 14 days. The leaves appear with the greatest frequency when the plants are making their most vigorous growth.

THE INFLORESCENCE

Since the name " head " is the usual agricultural term for the inflorescence of timothy, it seems better to follow common usage, even though this name may not have been generally adopted in botanical literature.

The head is a very contracted panicle. There are on it a very large number of subsessile spikelets, crowded closely together, extending outward from the axis, and forming a dense cylindrical inflorescence (*13, p. 10–11*).

At the base of each spikelet are the two glumes. The pistil and stamens of the single floret of each spikelet are inclosed in the lemma and palea. The two glumes, the lemma, and the palea are arranged alternately, like the leaves of a shoot, in two ranks (*4, p. 17–20*). The appearance of a timothy spikelet, with a floret in bloom, is illustrated in Plate 7, *C*.

The palea of the floret and the prophyllum of branch shoots in grasses are commonly regarded as homologous. This theory is based upon the facts that one stands between the rachilla and a floral branch, the other between the stem and a vegetative branch (*17, p. 118, 127*); the relative positions of the palea and of the prophyllum are the same, each having its back to the axis on which the branch is borne (*4, p. 17*); in grasses both the palea and the prophyllum are usually 2-nerved or 2-keeled, instead of having a single prominent midrib, like the leaves (*40, p. 59*).

On plants of some species of grasses having florets borne singly in the spikelets the florets are apparently terminal on the rachilla, instead of growing laterally as on plants of species having several florets to each spikelet (*17 p. 132*). In Plate 8, *D* and *E*, each floret or modified floret is growing at the tip of the abnormally elongated axis, which, it is assumed, represents the rachilla. Although the axes of these spikelets do not extend beyond the bases of the florets, the axis of each floret is at a slight angle to the rachilla, which indicates that in timothy the floret is not terminal.

The inflorescence of timothy has been fully described in various textbooks and other botanical publications (*13 p. 10–11; 29, p. 123; 18, p. 140–141*).

GROWTH OF THE HEAD

A timothy head emerges from the upper leaf sheaths of the culm when the shoot has attained about one-half of its final growth in length. A rudimentary head, however, can be found if the inclosing leaf sheaths are removed on a large and vigorous shoot several weeks earlier.

Timothy shoots were collected from an ordinary meadow at intervals of one week from May 1 to July 3, 1916. Five shoots, each with a head or with the rudimentary part from which it develops, were examined on May 1; on each later date when observations were made 10 shoots were examined. The average length (in inches) of timothy heads on different dates in 1916 was as follows: May 1, 0.09; May 8, 0.10; May 15, 0.12; May 22, 0.22; May 29, 0.59; June 5, 1.86; June 12, 2.83; June 19, 3.52; June 26, 3.76; July 3, 3.70.

The heads made their most rapid growth in length from about June 1 to 20. The culms, which also made a relatively rapid growth in length during the same period, continued to grow for about three weeks after the heads had ceased to increase in length.

In another series of measurements, made in 1916, of 14 timothy shoots, the average date on which the heads had completely emerged from the upper leaf sheaths was June 19, when the shoots had grown to 53.9 per cent of their final length.

At the time when these 14 heads had just emerged from within the inclosing leaf sheaths their average length was 3.9 inches. On

July 28, more than one month later, the average length of the same heads was 3.95 inches. This shows that timothy heads practically complete their growth in length by the time they have emerged from within the upper leaf sheaths of the shoots.

LENGTH OF TIMOTHY HEADS

Webber has shown that there is a variation in the lengths of the heads of the plants of some different varieties of timothy (*42*, *p. 349–351*).

The length of heads of plants growing in a comparatively rich soil, and especially in new meadows, is much greater than of plants growing under less favorable cultural conditions.

On July 19, 1916, all the heads on shoots growing in a typical square-foot area in a 3-year-old timothy meadow were measured. The lengths of the heads ranged from 0.4 to 3.8 inches, and the average length was 1.7 inches. From another meadow, sown in the preceding season, a number of typical heads were collected; they were from 3 to 4.8 inches long, and the average length was 3.7 inches. From along the edge of another field, where soil conditions were very favorable for a large and vigorous growth of the plants growing there, one head (an exceptionally long one) was collected which measured 11.2 inches in length. The lengths of the heads in the two former groups are more nearly typical of the heads of timothy plants growing in ordinary meadows.

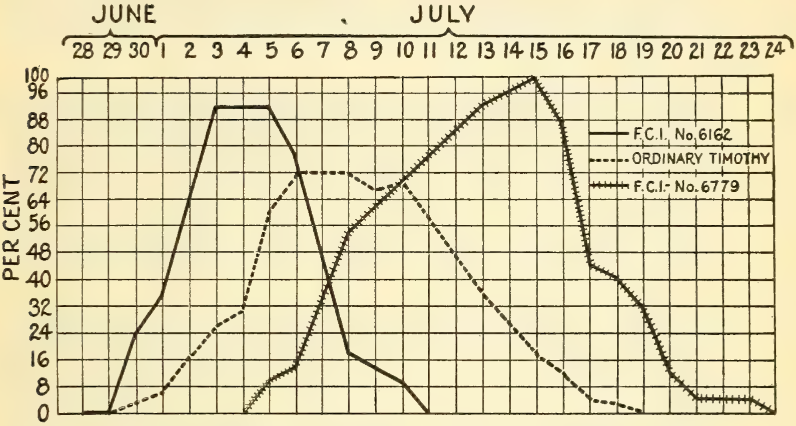
TIME WHEN TIMOTHY FLORETS BLOOM AND SEEDS MATURE

Timothy florets bloom in northern Ohio during the latter part of June and the early part of July. Within a few weeks, late in July or early in August, the seeds mature. The time when the florets bloom and the seeds mature varies slightly in different years, because of different seasonal conditions (*5*, *p. 330–333*). Figure 7 shows that there is also some difference in the time when plants of different selections or varieties bloom and mature in the same season.

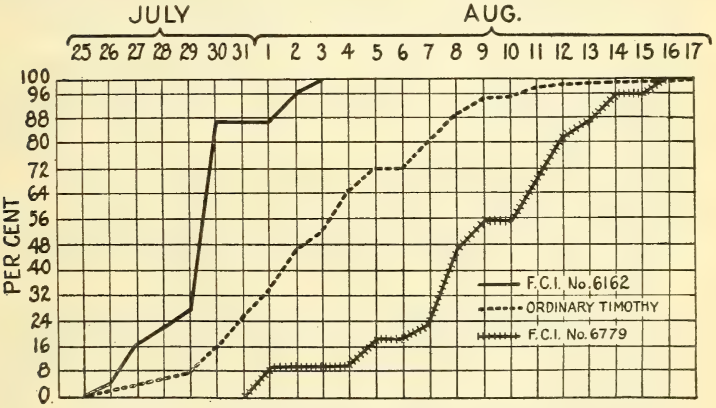
THE FLOWERING HABITS OF TIMOTHY

Observations of the flowering habits of timothy have been made at the timothy-breeding field station in nearly every season since it has been established. During the period from June 22 to July 7, 1914, a special study was made of this subject. Timothy plants were examined each night at intervals of two hours from 6 p. m. until 8 o'clock the next morning (*9*, *p. 299–309*).

When a timothy floret blooms, the anthers emerge first and then the stigmas. The anthers do not dehisce until after the stigmas of the same floret have been exposed for some time (*20*, *p. 35*). Any movement of the stem soon after the anthers have dehisced will cause the pollen to float away through the air in a miniature cloud. On the morning of June 28, 1922, exceedingly large numbers of timothy florets were in bloom. The air was very quiet until a little past 7 o'clock, when a breeze arose. When gusts of wind moved the stems of timothy plants growing in near-by plots the pollen could be distinctly seen rising in small clouds. It was observed that as the wind passed over a timothy meadow approximately half a mile away the clouds of pollen appeared as a haze over the field. Similar phenomena have been observed several times in fields of rye, but this is the only occasion at the timothy-breeding field station on which pollen of timothy has been observed to be carried by the wind in large enough quantities to form a cloud or haze visible at the distance of half a mile.



PERCENTAGE OF PLANTS IN FULL BLOOM



PERCENTAGE OF PLANTS MATURE

FIG. 7.—Comparison of the percentages of timothy plants in full bloom (upper part of graph) and of plants matured (lower part) on different dates in 1917, in a row plat of F. C. I. No. 6162, an early selection (continuous line); in a row plat of F. C. I. 6779, a late selection (line with cross marks); and in row plats of ordinary commercial timothy (dotted line). The first plant was in full bloom in these plats June 29 and the last one July 23; the first plant matured July 26 and the last one August 17

The fact that the stigmas of timothy emerge before pollen is released from the anthers of the same floret and the ease with which the pollen is distributed by the wind indicate that timothy is naturally cross-pollinated. Results obtained in experimental breeding support the theory that cross-fertilization of timothy does take place to some extent. On the other hand, it is not wholly self-sterile, since when the heads of any plant are inclosed in a paper sack during the blooming period some germinable seed is usually obtained, though a much smaller proportion of the florets produce seed than when pollination occurs under normal conditions (*15, p. 289–293*).

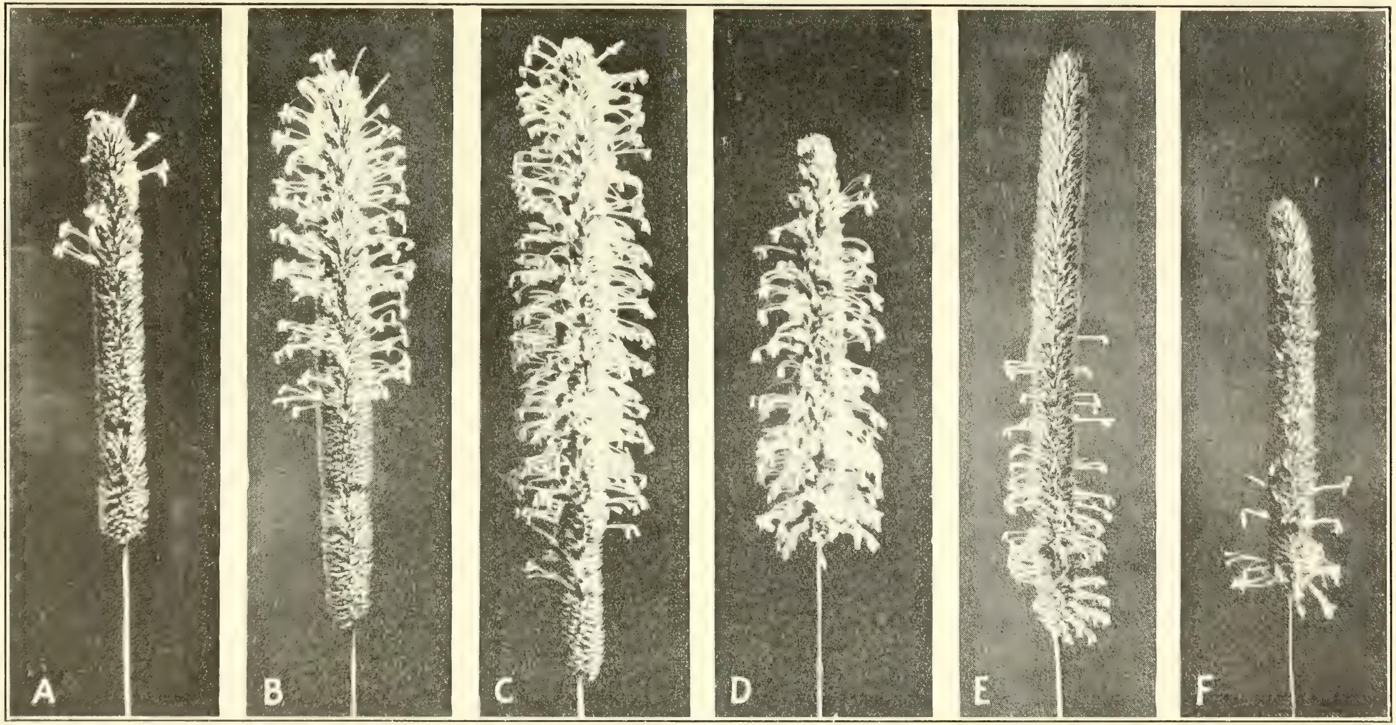
The florets growing in the upper part of a timothy head bloom first. Florets lower on the head come into bloom on succeeding days, the last to bloom being those growing near the base. The florets on a single head may continue to bloom during about 6 to 16 days. Timothy heads at different stages of bloom are shown in Plate 9.

Timothy florets begin to bloom in meadows of ordinary timothy in northern Ohio about June 15 or 20 and continue to bloom in large numbers until about July 10 or 15. The period during which florets are blooming in very large numbers, however, is about 10 days, most frequently from about June 25 to July 4, but varying a few days from this time, earlier or later, in some seasons. When weather and soil conditions are favorable for the development of shoots with heads during the late summer and fall, florets may bloom in relatively small numbers until late fall.

The greatest number of timothy florets bloom in the early morning hours, from about midnight until about the time of or soon after sunrise. The number of florets that bloom each day and also to some extent the time of blooming are affected by weather conditions, especially temperature. Clear weather and a minimum daily temperature of 60° F. or above are most favorable. When the weather is relatively cool, and especially if it is cool and cloudy or if there is a rainfall, timothy florets frequently fail to bloom.

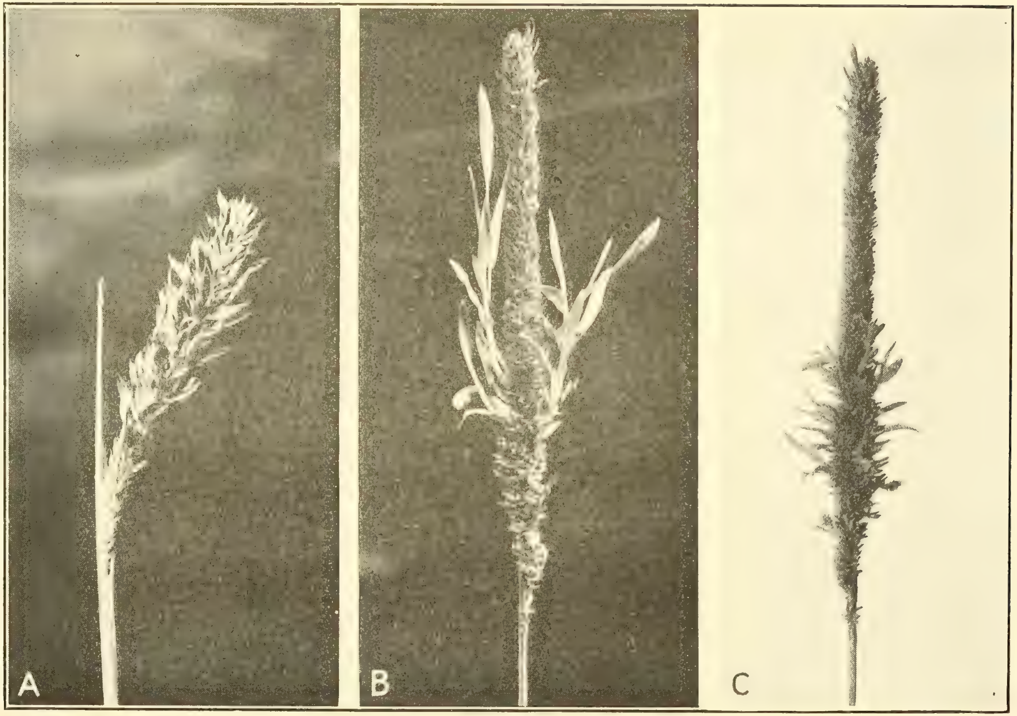
When timothy florets do not bloom on any particular day they are likely to bloom in large numbers on the day following, even though conditions are not most favorable. Thus on the morning of June 28, 1919, the sky was clear; the temperature during the 24 hours preceding 8 a. m., at the United States Department of Agriculture Weather Bureau station at Cleveland, Ohio, which is at a distance of 22 miles and at approximately the same elevation as the timothy-breeding field station, ranged from 56° to 66° F.; no timothy florets bloomed on that morning. On the morning of June 29, when the sky was again clear, timothy florets bloomed in medium numbers, though not in so large numbers as on some days, so that the meadows appeared somewhat purple in color, even though the temperature during the preceding 24 hours ranged from a minimum of 52° to a maximum of 61° F. When weather conditions remain very unfavorable, however, timothy sometimes fails to bloom for two days in succession.

Except when unfavorable weather conditions exist, the blooming of timothy may be regarded as a process continuing without interruption from day to day from the beginning to the end of the blooming period. This is illustrated by records obtained daily in 1921 from June 20 to July 3, inclusive. The minimum daily temperature during this period at the Cleveland Weather Bureau sta-



TIMOTHY HEADS AT DIFFERENT STAGES OF BLOOM

A and B are in early bloom, C and D are in full bloom, and E and F are in late bloom. Usually a week or more elapses from the time when the first florets of any head bloom until the late florets near its base have bloomed



THREE TYPES OF TIMOTHY HEADS

A.—A timothy head with florets, each having a single bract proliferated
B.—A timothy head with proliferous shoots
C.—A timothy head with branches. There are also a number of proliferating florets and proliferous shoots on this head

tion ranged from 60° to 72° F. Large numbers of timothy florets bloomed on each day during this period, except on the morning of June 29, when practically none bloomed; the minimum temperature during the preceding 24 hours had been 71° F., but the sky was cloudy, and there was a heavy rainfall in the afternoon of June 28. In most seasons there are more frequent interruptions in the blooming process on different days during the period when timothy meadows are at the height of bloom than there were from June 20 to July 3, 1921.

The color of a timothy meadow in bloom varies greatly at different times during the blooming period. These changes are chiefly due to changes in the color of the anther sacs at different times and to variations in the number of florets that bloom on different days.

PROLIFERATION IN TIMOTHY

Proliferation has been observed to manifest itself in the inflorescence of timothy in the ways described below:

Proliferating florets, each having one bract enlarged to resemble a leaf. Either the pistil or stamens, or both, are usually present.

Proliferous shoots, capable of developing directly into plants. In a proliferation of this type there are several leaflike parts, but no pistil or stamens.

Spikelets with elongated rachilla.

In addition to these three forms of proliferation, branches have occasionally been observed on the same heads bearing proliferating florets.

Proliferation in grasses is not peculiar to timothy. Goebel (*12, vol. 1, p. 178–185*) states that it may occur in *Poa alpina* and *P. bulbosa*. Hackel (*13, p. 31–32*) has observed this phenomenon in *P. stricta*, *Deschampsia alpina*, and *Festuca fuegiana*. Jenkin (*22, p. 418–419*) shows that the tendency to proliferation is especially marked in certain strains of *F. ovina;* he has also observed proliferation in *F. rubra*, *Cynosurus cristatus*, *Alopecurus pratensis*, and *Lolium perenne*. Other species could be added to these lists.

CONDITIONS UNDER WHICH PROLIFERATION OF TIMOTHY OCCURS

Ward states that proliferation occurs in "some grasses growing in high latitudes, or in mountainous regions, or in moist situations" (*37, p. 133–134*). Proliferation in timothy has been observed in northern Ohio almost exclusively on heads which develop during the fall months, and especially on those which appear during the last few weeks before growth is checked by cold weather. That proliferation does less commonly occur in timothy earlier than the fall months is indicated by occasional botanical specimens with proliferating florets which have been collected in other localities. In the Gray Herbarium at Harvard University there are two specimens of *Phleum pratense*, both with proliferating florets, collected during the summer months. One of them was collected by J. C. Parlin on the banks of the Androscoggin River, in Maine, August 16, 1906; the other was collected by Sereno Watson in Ruby Valley, Nev., at an altitude of 6,000 feet, in July, 1862. In the National Herbarium at the Smithsonian Institution, Washington, D. C., there is a botanical specimen of *Phleum pratense* with several proliferating florets, collected by Mrs. Agnes Chase along a woodland path at Riverdale, Md., July 4, 1912. In both herbariums all or nearly all other specimens of *Phleum pratense* with proliferating florets were collected during the fall months.

It has been observed that timothy plants with proliferating inflorescences are more numerous in some seasons than in others. In the fall of 1919 very few proliferations could be found on the timothy plants growing on the timothy-breeding field station at North Ridgeville, Ohio, while in the fall of 1920 they were quite numerous there.

The extent to which proliferation in timothy occurs apparently varies with differences in the cultural conditions under which the plants are grown. A record made on November 6, 1920, shows that in a series of broadcast plats of ordinary timothy on the station, 9.8 per cent of the growing heads had proliferations, whereas in a near-by series of cultivated row plats of plants grown from the same lot of seed which was sown in the broadcast plats, 35.5 per cent of the heads had proliferations.

On November 9, 1920, a record was made of the number and percentage of growing heads with proliferations on plants in a series of row plots of timothy selections all grown under the same cultural conditions. All plants in each one of the rows were propagated from seed of a single plant. These records are presented in Table 18.

TABLE 18.—*Number and percentage of heads with proliferations in row plots of different selections of timothy*

F. C. I. No.	Number of heads with—		Total number of heads	Percentage of heads with proliferations
	Proliferations	No proliferations		
9219	16	19	35	45.71
9220	15	0	15	100.00
9327	1	35	36	2.77
9334	1	23	24	4.16
9335	6	27	33	18.18
9822	10	13	23	43.47

The data show that there were much larger proportions of heads with proliferations in the plats of some selections than of others. These varying proportions may possibly be explained by different inherent tendencies in the plants. Another possible explanation is that, since not all of them bloom and mature at the same time, some of the selections may have been at the proper stage of development for proliferation to occur, while others either had not arrived at or else had passed that stage when conditions external to the plants were right to induce proliferation in timothy.

A shoot with proliferating florets is frequently more or less abnormal in other respects, having parts of the head bare of florets or having the base of the head partially inclosed in the sheath of the upper leaf of the shoot, which not infrequently has more leaves growing from the culm than typical shoots which produce heads in midsummer. A late shoot of this kind is shown in Plate 6, *C*.

Proliferating florets, which usually constitute only a small proportion of the total number of florets on any head, and normal florets in bloom often have been observed on the same head.

On all timothy spikelets which have been examined in which a proliferating floret was growing, the two outer glumes, which are a part of the spikelet and not of the floret itself, have never been found appreciably enlarged or modified into leaves.

PROLIFERATING FLORETS WITH A SINGLE ENLARGED BRACT

By far the largest proportion of timothy florets with evidence of proliferation have but one enlarged bract, like the florets on the head shown in Plate 10, *A*. In Plate 8, *A*, are shown three detached spikelets with proliferating florets, each with a single enlarged bract. A floret with this type of proliferation, from which the glumes of the spikelet have been removed, is shown in Plate 8, *B*.

Proliferating florets with one enlarged bract usually have either a pistil or stamens, or both, though these frequently appear somewhat withered or in other ways do not appear quite normal. On November 17, 1920, a floret of this kind from each of nine heads was examined. On eight, or 88.8 per cent, of these florets pistils or stamens were found. Enlarged ovules, apparently representing seed in the early stages of growth, have been found in proliferations with one enlarged bract.

In a group of 25 florets which were examined, each with a single enlarged bract and with a pistil or stamens, it was in every case the lemma which resembled a small leaf; the palea was of normal or approximately normal size and form.

PROLIFEROUS SHOOTS

Proliferations of timothy, which in appearance resemble small innovations grown from vegetative buds, are designated here as proliferous shoots. They are fundamentally different from the ordinary proliferating florets, each of which has a single enlarged bract. There are several proliferous shoots on the head shown in Plate 10, *B*.

The most easily apparent difference between a proliferous shoot and an ordinary proliferating floret is that the former has several leaflike parts instead of a single one. As has been stated, in a proliferation of the latter type it is the lemma which is enlarged, while the palea appears normal. In a proliferous shoot, on the other hand, the lemma is enlarged very slightly, and in some cases apparently not at all, while the part above it resembles a small leaf. Since, in proliferous shoots, buds have sometimes been observed in the axils of leaflike parts, they may evidently be regarded as true leaves.

The empty glumes of the spikelets of timothy during the course of this investigation have never been observed to become modified through proliferation.

In a proliferous shoot there are no stamens or pistil. It would obviously be impossible for a typical proliferating floret, with one leaflike part and with a pistil and stamens, to become transformed later into a typical proliferous shoot with several leaves but with no pistil or stamens.

REPRODUCTION FROM PROLIFEROUS SHOOTS

A proliferous shoot, unlike a proliferating floret with a single enlarged bract, is capable, under suitable conditions, of developing into a timothy plant.

On November 13, 1920, two groups of plants were taken from plats on the station and transplanted to a bench in a greenhouse. On each one of the first group of 23 plants there was one head with proliferating florets, each with a single enlarged bract. On each of the second group of 12 plants there was a head having a number of proliferous shoots. When the plants were transplanted the stems with proliferations were bent over and the heads partially covered with soil. From the 23 heads with single bract proliferations no timothy plant developed. From the 12 heads in the second group plants developed directly from one or more of the proliferous shoots on 7, or 58.3 per cent, of the heads.

Although proliferous shoots under the proper conditions readily take root and develop into timothy plants, on only two occasions during this investigation were timothy heads with proliferations observed in meadows of ordinary timothy on stems bent over so the heads were in contact with the soil. On neither one of them had any of the proliferations taken root at the time when they were observed.

PROLIFEROUS SHOOTS NOT VIVIPAROUS

The occurrence of vivipary is sometimes referred to in the botanical literature of grasses (*22, p. 418–419*). Used accurately as a botanical term, vivipary means the germination of a seed while it is still attached to the parent plant, though the term has commonly been used incorrectly to describe the development of what are designated in this bulletin as proliferous shoots. The evidence presented in the following paragraphs shows that in timothy the proliferous shoots are not viviparous in their origin.

On the primary shoot of any timothy plant developed from seed the first leaf blades are comparatively long and narrow, like those on the seedling at the right in Plate 8, *C*. On a timothy shoot developed from an ordinary vegetative bud the first leaf blades are relatively short and broad, like those on the shoot at the left in Plate 8, *C*. The first leaves of the proliferous shoot in the center of this illustration are very similar to the first leaves of the vegetative shoot at the left and quite dissimilar to the first leaves of the seedling shown at the right. This is very strong evidence that the proliferous shoots of timothy do not develop from seed.

In November, 1920, a timothy plant having a head with several proliferous shoots was examined. A small vegetative bud was growing in the axil of one or more of the leaves on several of these shoots. On one of them a well-formed bud was growing in the axil of the outer scale, corresponding to the lemma, which was shorter than the glumes of the spikelet and which was modified, if at all, but very slightly. This may be regarded as direct evidence that proliferous timothy shoots represent a vegetative growth.

ELONGATION OF THE RACHILLA

Early in November, 1920, a number of timothy heads were observed on which there were one or more spikelets with the floret borne on an elongated axis, which apparently represented the rachilla. This elongation of the rachilla may be regarded as one form of proliferation, which is much less common than the enlargement of bracts to form leaves. A similar, if not an identical, form of proliferation has been observed in *Agropyron cristatum* (*30, p. 423*).

Three timothy spikelets, photographed November 10, 1920, each bearing a floret on an elongated rachilla, are shown in Plate 8, *D*. The bracts of the florets were somewhat thickened but in other ways resembled the lemmas and paleas of florets growing in the usual position. The floret at the right had recently bloomed, as is indicated by the three anthers attached to it by their filaments.

A rare form of proliferation is illustrated in Plate 8, *E*. On each of the three spikelets shown the floret was borne on an elongated axis, which probably was the rachilla. On each one of the three florets the lemma resembled a small leaf.

HEADS WITH BRANCHES

Timothy heads with branches develop rarely. They have been observed to be associated with the development of proliferous florets. On November 9, 1920, a timothy head, shown in Plate 10, *C*, was collected on which there were six small branches, each bearing a number of spikelets, the bracts of which were relatively small. There were also a number of proliferating florets on the same head. This one and a second head with branches less well developed were the only ones observed during the investigations made of proliferation of timothy in the fall of 1920.

EFFECT OF LENGTH OF DAY ON GROWTH OF TIMOTHY

In any timothy meadow, during the spring and early summer, the stems of the plants grow in length, heads appear, florets bloom, and seeds mature. Each phase of growth occurs at approximately the same time on all the plants in the meadow. The process is repeated annually, with but relatively slight deviations in the dates when the same stages of growth are attained in different years. Evidently there is some very close relationship between climatic conditions at certain times in the season and the phases of growth which normally occur when these particular conditions exist. It is true that the stems may become elongated and that heads with florets in bloom can be found in smaller numbers in timothy meadows in the fall, several months after the usual time, but, as has already been stated, these late shoots do not usually grow in a normal manner.

GROWTH THROUGH THE WINTER WITH NORMAL PERIOD OF LIGHT

Plants of many kinds bloom and produce seed only at certain times in the season when the length of day is right for these processes to occur. Some varieties bloom and produce seed in midsummer, when the days are long and the nights are short, whereas other varieties of the same species may not produce seed until fall when the days are short. This response in the behavior of plants to variations in the length of the period of daily illumination is called *photoperiodism* (*11*, *p. 871*).

When timothy plants are transferred in late fall or winter from the field to a greenhouse where temperature and soil conditions are favorable, growth occurs, but in a manner much different from that in the field during the spring and early summer.

On January 5, 1922, a number of timothy plants were taken from a field. Some of them were transplanted again to a row in the field on the station; the remainder were transplanted to a greenhouse. During the period from January 5 until April 4 a new leaf appeared on each one of the shoots observed on the plants in the greenhouse at an average interval of 8.7 days. This record shows that the conditions there were such that a relatively vigorous vegetative growth occurred.

Five of the plants transplanted to the greenhouse were retransplanted to a coldframe on April 4; five other plants were retransplanted to the field on May 20 in a row plat adjoining the one to which plants were transplanted directly from the field on January 5. A record was obtained of the date when the first head appeared on each plant. When the shoots on the different plants had completed their growth they were examined, and the number of leaves and of elongated internodes on one shoot marked for observation on each plant were counted. These data are presented in Table 19.

TABLE 19.—*Characteristics of timothy plants taken from a field January 5, 1922, and grown under different conditions*

Treatment given the plants	Number of plants used	Average date when first head appeared	Average number of leaves on shoots observed	Average number of elongated internodes in the culm
Grown in the field during the entire period	7	June 5	17.3	6.4
Transplanted from field to greenhouse Jan. 5, 1922:				
(*a*) Retransplanted to coldframes Apr. 4	5	June 9	25.6	11.4
(*b*) Retransplanted to field May 20	5	June 7	23.2	9.8

In the experiment conducted in 1922, described in Table 19, the plants grown in the greenhouse were different from those grown in the field. There was, therefore, some opportunity for small experimental errors, owing to variation inherent in different plants. In 1923 a similar experiment was again conducted. In the latter season, however, three plants were taken from the field on January 19, each of which was divided into two parts; one part was transplanted to a greenhouse and the other to the field, where it continued its growth under normal conditions. The results are presented in Table 20.

TABLE 20.—*Characteristics of timothy plants taken from the field January 19, 1923, and grown under different conditions*

Treatment	Average date when first head appeared	Average date of full bloom	Length of stem, including head	Average number of elongated internodes in haplocorm and culm
			Inches	
Part of each plant transplanted to the field Jan. 22	June 11	June 29	41.9	6.5
Part of each plant transplanted to the greenhouse Jan. 23 and retransplanted to the field May 26	June 9	June 25	29.8	10.3

EFFECT ON LEAF GROWTH

In the experiment conducted in 1922 the number of leaves per shoot was much larger on those plants which continued their growth during the winter in the greenhouse than on the plants which remained in the field. This record corresponds with results obtained from similar experiments in earlier years.

EFFECT ON GROWTH OF ELONGATED INTERNODES

In both 1922 and 1923 elongation of the internodes did not occur in the stems of the plants grown in the greenhouse until several weeks after they had been transplanted from the field, yet elongated internodes did begin to form earlier than on the plants which remained in the field. In each season there was an average number of approximately 6.5 elongated internodes in the haplocorm and culm of shoots with heads on plants grown in the field, while on plants grown in the greenhouse the number of elongated internodes per shoot varied approximately from 9.5 to 11.5.

The lower internodes of the stems of plants grown in the greenhouse were relatively short and did not increase in length from the lower part of the culm upward, neither did haplocorms form at the bases of these stems in the way in which they develop on plants in the field in late spring and early summer. The appearance of stems grown under both conditions is illustrated in Plate 11.

On a large proportion of those timothy stems in meadows which become elongated and produce heads late in the season during the autumn months supernumerary elongated internodes are quite common, and either there is a relatively small haplocorm or else it is entirely absent. In these respects the shoots which began their growth in length in the greenhouse abnormally early in the spring resemble the shoots which become elongated in the field in late fall.

EFFECT ON TIME OF HEADING AND BLOOMING

In 1922 the average date at which the heads appeared on the plants grown in the greenhouse during the winter was a few days later and in 1923 it was 2.6 days earlier than on the plants grown in the field. In both seasons the difference was relatively small.

GROWTH UNDER LONG AND SHORT DAILY PERIODS OF ILLUMINATION

It may be assumed that the partial delay which occurs in the time of elongation of the stem and the more definite delay in the date of heading and blooming on timothy plants which make continuous and vigorous vegetative growth in the greenhouse during the winter is due to the tendency for these processes to take place only when the days are relatively long, as in late spring and early summer, rather than when the days are shorter. In order to test this theory more carefully under conditions where length of day was the only varying factor an experiment was conducted in the winter of 1923–24 in a greenhouse where the length of daily illumination could be controlled. Each one of a number of timothy plants was divided into two parts. Beginning on or approximately on November 10, 1923, one part of each was grown on a bench where the length of daily illumination was extended by means of electric lights so that the plants were illuminated for several hours after nightfall. The other parts of these plants were grown in the same greenhouse. Each day at 4 p. m., they were placed in a large box from which light was excluded and in which they remained until 9 a. m. the next day. The former group of plants received, during the time the experiment was conducted, approximately 16.5 hours of light daily; the latter group of plants were in the light for 7 hours each day.

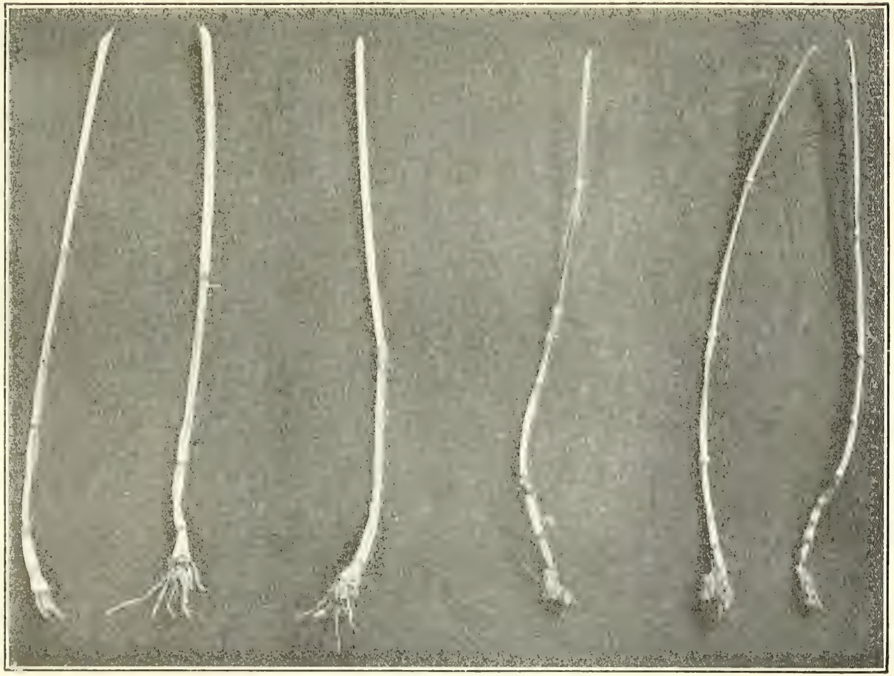
On February 18, 1924, a typical plant grown under each period of illumination was photographed; they are shown in Plate 12. Each one of these plants was propagated vegetatively from the same original plant; any differences in them are therefore due to different conditions for growth and not to variations in the plants themselves.

On all of the plants used in this experiment which received light for 16.5 hours each day the shoots made a comparatively rapid growth in length. On the plant shown in the illustration, four of the shoots produced heads. The total lengths of these shoots, including the heads, were, respectively, 23.75, 29.40, 29.50, and 35.20 inches. Three of the shoots had six elongated internodes each and the fourth one had seven. The average number of elongated internodes was 6.25 per shoot, which is practically the same as on shoots which produce heads in meadows at the normal time in the spring.

At the base of each fertile shoot, and also at the base of each one of five elongated shoots on which heads did not develop, on the plant grown under relatively long-day conditions there was some enlargement in the diameter of the stem, owing to the formation of a haplocorm.

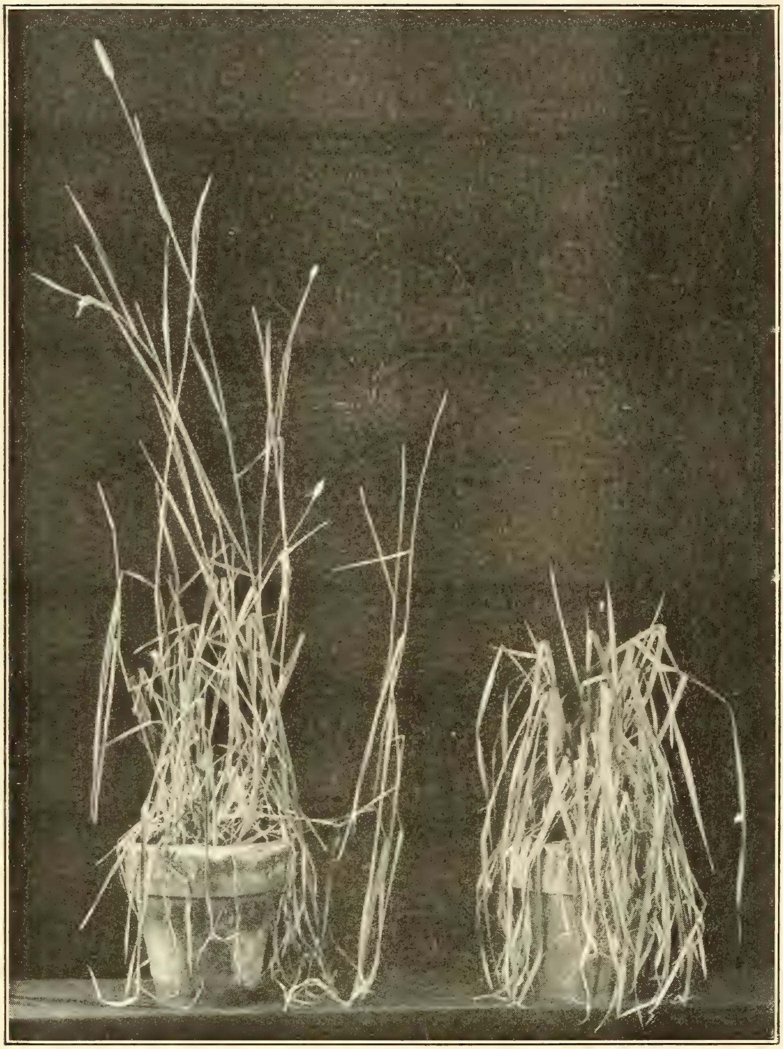
Florets on one of the heads of the plant shown in the illustration and also on one head of each of two other plants grown with 16.5 hours of light each day were in bloom on or had bloomed prior to February 18, 1924.

Although the plants which received light for seven hours each day made a vigorous vegetative growth, the internodes of the stem did not become elongated, nor was there any development of the inflorescence; their growth resembled that of plants in the field during the relatively short days of late fall. On plants exposed to light 16.5 hours daily, on the other hand, the stems became elongated, heads de-



NATURAL AND ARTIFICIAL GROWTH OF TIMOTHY

The three bases of timothy stems at the left were produced on a plant which grew out of doors under normal conditions. The three stems at the right are from a part of the same original plant which was transplanted January 23 to a greenhouse where conditions were favorable for a vigorous vegetative growth during the winter months. Note the numerous relatively short internodes and the absence of haplocorms on the stems grown in the greenhouse. Each stem base is 8 inches in length



A STUDY IN EFFECT OF LIGHT

Two timothy plants, propagated vegetatively from the same original plant, which were grown under different periods of daily illumination for a period of slightly over three months. The plant at the right was in the daylight 7 hours each day, and the one at the left received natural or artificial light 16.5 hours each day. None of the stems became elongated on the plant grown under the shorter day, while on the plant grown under the longer day the internodes of the culm became elongated and on four of the shoots heads were produced veloped, and florets bloomed in very much the same manner as on timothy plants in meadows during the longer days of late spring and early summer.

DIFFERENT PHASES OF GROWTH IN RELATION TO PHOTOPERIODISM

Different phases in the growth of some plants respond to differences in the daily period of illumination in different ways (*11, p. 917–919; 36, p. 314*). In timothy three distinct gradations in as many different phases of growth, in response to variations in the daily period of illumination, were observed during the course of this experiment.

The growth of the leaves is affected relatively little by variations in the length of the period of daily illumination within the limits described for these experiments.

The growth in length of the stems does not take place under the minimum period of illumination used in these experiments, i. e., 7 hours each day; yet elongation of the internodes of the culm does occur several weeks earlier in the greenhouse, where normal conditions of lighting exist and where other conditions permit continuous growth to take place, than on plants growing in the field.

The process of the development of the inflorescence is very sensitive to the length of the daily period of illumination. Heads did not appear, nor did florets bloom, on plants which had made continuous growth in the greenhouse with the natural period of illumination until at practically the same time in the spring when these processes took place on plants which had grown under normal conditions in the fields.

SUMMARY

A timothy plant is composed of all of the growing shoots which have developed either from a seed or from the detached vegetative part of another plant. In a plant several years old there may be a number of closely associated shoots or groups of shoots which have no vital connection with one another, but which, nevertheless, represent branches which have originated from the same primary shoot.

The position of a timothy seedling tends to become adjusted, in relation to the surface of the soil, as the seed is sown at different depths, ranging from the surface down to about 1 inch below it. Within these limits, through elongation of the mesocotyl, the base of the primary shoot of the plant develops near the surface of the soil, irrespective of the depth at which the seed was sown.

When timothy is growing under natural conditions the seeds mature, fall to the ground, and a large proportion of them may germinate during the late summer months. A shoot originating from a seed which germinates at this time continues its growth until the following season. If an inflorescence develops on it, seeds will mature in midsummer, and within a few weeks or months the shoot becomes entirely dry, about one year or a little more than a year after it began its growth. If a timothy seed is sown in early spring and if conditions are favorable for growth, the primary shoot of the plant may produce seeds and complete its growth in the same season.

A timothy plant continues to perpetuate itself indefinitely through the growth of new branches from buds in the axils of leaves, generally near the bases of the older shoots. Buds and branches rarely appear, in the types of plants which grow in meadows in America, at nodes situated between the elongated internodes of the culm. A branch shoot may be called an innovation from the time when it develops from the bud up to the time when any of the internodes become elongated or secondary branches form on it. In ordinary meadows buds expand into lateral shoots in the largest numbers in midsummer, about the time when seeds are maturing. A shoot developed from a bud at this time, like one originating from a seed, continues its growth until the following summer, when it also may produce seeds, and a few weeks or months later ceases growth. In this manner, through vegetative reproduction, a timothy plant may perpetuate itself for an indefinite number of years. It differs from perennials like trees or shrubs, however, since each year there is a new set of shoots, with new roots, which do not retain a vital connection with the shoots which were growing on the plant in previous years.

The axis or stem of a shoot which expands from a bud at some time in the summer ordinarily grows hardly half an inch in length during the following fall, winter, and early spring. The non-elongated internodes which develop on it during this period form the proaxis.

Beginning about May 1, under climatic conditions similar to those in northern Ohio, the internodes which develop after that time become elongated. The lowest one, less frequently two elongated internodes, become enlarged in diameter also and form the haplocorm. Above it, the 4 to 6 or 7, most commonly 5, elongated cylindrical internodes form the culm. On a shoot producing a head the internodes of the culm continue their growth in length until after the florets have bloomed and until a short time before the seeds mature.

The total number of internodes and also of nodes and leaves which develop on a shoot during the entire period of its growth commonly varies from about 15 to 25, though the number is frequently either below or above these limits. The number of non-elongated internodes in the proaxis varies in proportion to the length of the growing period, being considerably greater on shoots which begin their growth in midsummer than on those which do not begin growth until late in the fall or early in the following spring. The number of elongated internodes in the haplocorm and culm does not vary to more than a slight extent on shoots with heads which develop at the usual time in midsummer. On shoots which produce heads in the fall the number of internodes in the culm is more variable. The florets bloom and seeds mature at nearly the same time in midsummer, whether the shoot began its growth from a seed or from a bud in the preceding summer or fall or early in the spring of the same season.

During the summer or fall in any timothy meadow which has not been mowed during the season two distinct types of elongated shoots may be found in varying proportions. Those fertile shoots on which heads are borne which have already been described represent one type; the shorter shoots of the other type produce no inflorescences. These sterile shoots grow, and the number of internodes and leaves continues to increase until checked by drought, cold weather, or in some other way. At the tip of the sterile shoot during late fall the leaves grow from nodes which are close together in much the same way as on the proaxis. In the axils of these apical leaves which are not separated by elongated internodes there are often buds which expand to form innovations. If one of these shoots is bent over and the tip partially covered with soil, the innovations readily take root and will develop into normal plants.

A timothy shoot which bears a head may develop from a bud on a sterile shoot, or a shoot of the latter type may originate from a fertile shoot.

In new meadows on fertile soil, and especially if each plant has ample space for development, most of the shoots may produce heads. As the meadow becomes older, or in meadows located where the soil is not very productive or where the stand of plants is relatively dense, the proportion of fertile shoots is less and of sterile shoots greater than in meadows where conditions are favorable for a large and vigorous growth. The number and proportion of both types of shoots may also be affected by hereditary tendencies; plants of some varieties produce a larger proportion of short, leafy shoots than others.

Timothy roots are slender and fibrous, many of them having numerous fine branches. Most of them grow within a few inches of the surface of the soil. On an innovation the roots develop soon after it expands from a bud, and it soon becomes independent of the primary shoot. The roots are not perennial. The life of all of the roots on a shoot, like that of the shoot itself, does not extend beyond the season following the one in which their growth began, and it may even be limited to a single season.

The term "haplocorm" has been applied to the enlargement at the base of a timothy shoot. A haplocorm is usually composed of one or two elongated internodes. A haplocorm develops on practically all timothy shoots which become elongated at the normal time during the late spring, whether the plant is growing on a moist, fertile soil or whether conditions are less favorable for a large and vigorous growth. On those late shoots which become elongated during the fall months the haplocorm is frequently either not well developed or absent altogether.

Buds at nodes immediately below or above the haplocorm very commonly develop into innovations. Though the evidence is not conclusive, it seems not unlikely that nutrients stored in the haplocorm may have some effect on the growth of new shoots which develop at adjoining nodes. On the other hand, vegetative reproduction also very frequently occurs through buds in the axils of leaves of shoots before the haplocorms have developed on them. Therefore, although the haplocorm under some conditions may have some relation to the growth of young shoots, it is not essential to the vegetative reproduction of timothy.

A timothy leaf may develop at any time during the growing season, remain green for several weeks, and then dry up as new leaves appear. During the spring, summer, and early fall a new leaf appears on each shoot at intervals of about 8 to 14 days, and a period of about 50 to 60 days elapses from the time when the blade first appears until it becomes dry. During the late fall and winter months, when the plants are more or less dormant, the leaves remain green for a considerably longer time.

On any growing shoot there are usually at any time from about four to six leaves with green or partially green blades until a short time before the shoot completes its growth, when the number of green leaves begins to diminish.

The term "head" is applied to the inflorescence of timothy, since it is the name in general use by farmers and by agricultural writers.

The rudimentary head may be readily distinguished early in the spring within the leaves of a young shoot. The head practically completes its growth in length before it emerges from the sheath of the upper leaf. Under conditions like those in northern Ohio the florets begin to bloom late in June, when the shoot has grown somewhat more than half of its final length, and the seeds mature late in July or early in August. Although the available evidence indicates that timothy is commonly cross-pollinated, the florets are not wholly self-sterile, since relatively small proportions of them produce seeds when the heads are inclosed in paper sacks throughout the blooming period.

When soil and climatic conditions are favorable for growth throughout the season, heads appear on shoots of timothy plants in smaller numbers at any time during the autumn. Heads on these shoots are frequently more or less abnormal, especially during the late fall. Proliferation may occur in various forms, usually manifesting itself by the modification of a single bract—the lemma—which appears as a small leaf. Less frequently the proliferation resembles a vegetative shoot, called a proliferous shoot. If partially covered with soil, one of these proliferous shoots will readily root and continue growth as a plant. Other forms of proliferation, such as elongation of the rachilla, occasionally develop.

Different phases of growth in timothy respond in different ways to variations in the number of hours of light to which the plants are exposed each day. The growth of leaves proceeds at much the same rate, if temperature and soil conditions are favorable, whether the days are relatively long or short. Elongation of internodes of the culms does not occur when the plants are exposed to light for 7 hours each day. When, however, plants are grown under favorable conditions in a greenhouse during the winter and early spring, with the normal number of hours of light each day, elongation of the internodes begins to take place several weeks earlier than on plants in the field. The development of the inflorescence is more sensitive in its response to the daily period of illumination. Heads appear and florets bloom on plants which make vegetative growth in the greenhouse during the winter and early spring at practically the same time as on plants which remain in the field in a more or less dormant condition during the winter months.

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